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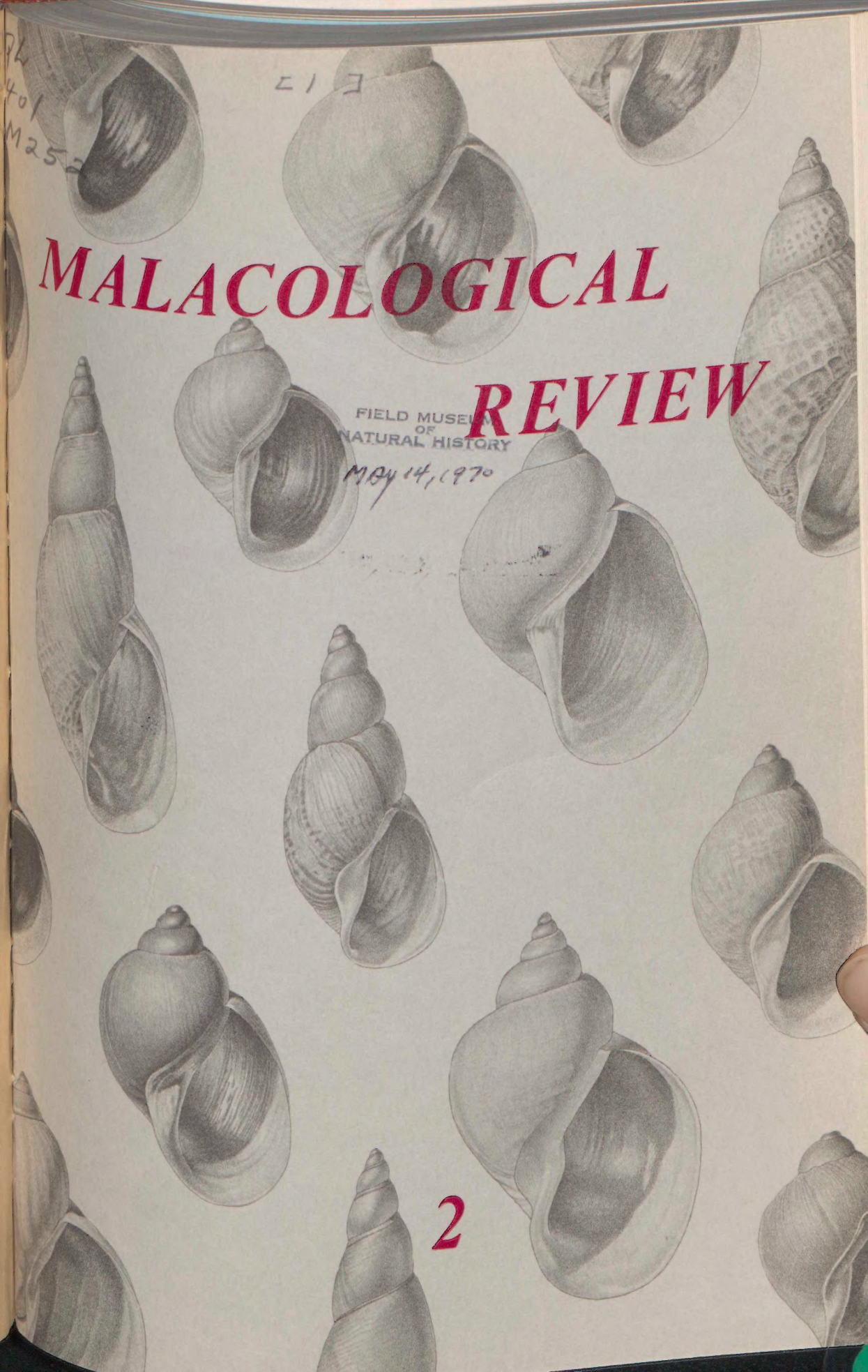

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ILLUSTRATED BIOMORPHOLOGY OF THE *"ANGULATA"* LAKE FORM OF THE BASOMMATOPHORAN SNAIL *LYMNAEA CATASCOPIUM* SAY[1]

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ILLUSTRATED BIOMORPHOLOGY OF THE *"ANGULATA"* LAKE FORM OF THE BASOMMATOPHORAN SNAIL *LYMNAEA CATASCOPIUM* SAY

INTRODUCTION

The primary aim of this publication is to place on record knowledge of the kind most needed to advance our understanding of the "pulmonate" freshwater snails of the Lymnaeidae and other "higher" Basommatophora (Limnophila; or, Hygrophila-Basommatophora-Pulmonata; or, Lymnaeacea-Basommatorphora-Euthyneura). The study originated and received support largely on consideration of the public health, medical, veterinary and economic importance of basommatophoran snails, and on consideration of the widespread concern of malacologists, parasitologists and others, about the perennial lack of a source of satisfactory taxonomic information on species of special importance, and on the species generally.

The Limnophila, as intermediate hosts of parasitic trematode worms, are the vectors of diseases of vertebrates on a vast worldwide scale, and each of the 4 families of the group are involved in this phenonemon. Each family is important in particular ways in relation to the broad biological implications of this problem. The Lymnaeidae and Planorbidae are the subject of large literature. They are essentially ubiquitous and commonly very abundant in diverse freshwater habitats in nearly all parts of the world. Consequently, they regularly become involved in many kinds of research which relate to aquatic biology and invertebrate zoology. The lymnaeids present a taxonomic species-problem of especially great magnitude, while the planorbids include vectors of human schistosomiasis (bilharziasis), a serious disease affecting millions of people over large geographical areas. The Physidae and Ancylidae are of relatively restricted geographical or ecological occurrence, and receive attention from few researchers. However, the physids are of special interest in showing an extreme kind of species-variation similar to that which generally makes taxonomic problems in the Limnophila exceedingly difficult, while the ancylids may hold a key position in relation to basic questions about evolution of the higher Basommatophora, especially of the Planorbidae.

Our understanding of the Limnophila is inadequate primarily because the research challenge they present is too great in relation to the practical considerations which usually face interested workers. It is true, nevertheless, that serious failings in this field have resulted from neglect and misrepresentation of the morphological problem which underlies the total problem in question. Malacologists generally have not emphasized adequately the need for the most basic kind of morphological research, and in large part have left this and other problems in basommatophoran biology to others, e. g., parasitologists, whose primary research goals are not malacological. Malacologists all too generally have limited their contributions on Basommatophora to taxonomies erected on fragmentary and often inaccurate morphological data. It has not been sufficiently acknowledged that in order to achieve satisfactory knowledge of any one family of the Limnophila, we must advance understanding of the Basommatophora as a whole, and that research failings regarding the whole, limit understanding of particular families. It should be apparent that a comprehensive, detailed and accurate body of morphological data would have to be established before adequate research can be done on many aspects of the biology of the snails, and before adequate taxonomies can be proposed. Without such a body of data we would not

be able to entertain many general and specific questions on the function, adaptive significance, homology and terminology of organs. As a first step, which has never been taken previously, the morphology of at least one basommatophoran species would have to be made thoroughly known, so as to set a working comparative standard. This publication is an attempt to make such a step. It is hoped that insofar as it fails to meet the stated goals, it will incite others to attempt to do so.

To my knowledge, not one organ-system of any basommatophoran species has been described in all important or relatively gross comparative respects. Of special concern is the reproductive system, which is of outstanding importance in comparative terms. It is the subject of the major part of the morphological and taxonomic literature, but neither the hermaphroditic, male, or female systems of any species seems to have been described fully in essential comparative details of form and internal structure. The male copulatory apparatus, despite a great emphasis placed on it in taxonomic works, generally has not been subject to careful comparative study, and even the structure of the presumably basic "simple" type of penis, which occurs in different families of Limnophila, has never been investigated thoroughly in any species. Furthermore, one region of the reproductive system of fundamental concern in comparisons between families generally has been seriously misrepresented in the literature. This is the region of separation of the male and female systems from the hermaphroditic tract. The term "carrefour" has been applied to this region, or sometimes to part of the female tract located there. The structural features of this region show different degrees of complexity in different families. Accurate knowledge of this region might well be of critical importance in elucidating the evolutionary origins of the families and relationships among them. Such knowledge would be essential also to revealing unknown critical aspects of basic reproductive processes in the snails, and to understanding adaptive changes that have led to mechanisms that permit or insure both cross- and self-fertilization in a system that is also complexly adapted to producing egg masses. As to other organ systems, the circulatory system is especially poorly understood because the venous system has been largely ignored, and implied to be not very well organized and of little critical importance in controlling blood flow. None of the published diagrams or descriptions of basommatophoran "pallial" venous circulation I have seen accounts for certain basic, gross structures that would be essential to transporting the large volumes of venous blood that must come from the 2 primary hemocoels of the body to the region of renal circulation and to the heart. Knowledge of the venous circulation could not only be of importance to understanding essentials of function and physiology, but to making fundamental anatomical comparisons between the families and to elucidating the origin of the Basommatophora. Relatively thorough descriptions of the arterial system and the nervous and digestive systems of one or more species of Limnophila have been published, but in all cases known to me there are significant gaps in the information given. The excretory and muscular systems generally have been slighted in the literature, and I have not found a truly detailed and comprehensive account of either of them. Even the radula and shell, despite a large literature on them, have not been subject in any species to the sort of thorough and comprehensive investigation that is to be desired for broad and specific comparative purposes. The foregoing criticisms apply even though there is a fairly large body of descriptive anatomical detail in the basommatophoran literature. Some excellent accounts of particular species do exist, and there is even considerable published information on microanatomy and histology. Nevertheless, much of such information cannot be utilized properly in comparative work because it has not been given in relation to entirely coherent or reasonably

complete accounts of the organ-systems it concerns, or in relation to essential facts about anatomical topography of the whole animal. Furthermore, there is a great need for reinvestigation, confirmation and clarification of many details that have been reported by authors; all too often doubt must be cast on what may be valid, especially in respect to histology, because it is associated with gross discrepancies or errors in the context in which it is given. The attempts to distinguish between published facts and errors in this field presents a considerable problem. A number of serious misconceptions about basommatophoran anatomy have been promoted by the uncritical acceptance by a succession of authors of each other's erroneous claims. This is especially true of the female reproductive system, and the carrefour in particular.

Failings in this field result in very large part from neglect or inadequate use of dissection as a research technique. Workers commonly have combined a rough dissecting technique with the study of serial sections. They usually have carried out dissection to a point, falling far short of a microanatomical level, and then have failed to use the section-method to reconstruct essential anatomical features skipped over in dissection. This situation has resulted in a relatively unexplored "territory," which falls between the macroanatomical and microanatomical levels. This is of concern because that "territory" is of the utmost importance in comparative anatomy in this field. Reconstructions from serial sections have been extensively used by the authors of some major modern taxonomic works in various Basommatophora, in an attempt to make anatomical comparisons between species and various taxa, but the results are crude and of little value for many of the comparisons attempted. In those works, it seems that it was intended to bypass the time-consuming, painstaking effort which critical dissection requires, by resorting to a supposedly quicker, easier and superior method. The advantages of that method are mostly illusory, however, for to be adequate it also must be applied, as a rule, with painstaking, time-consuming effort. There is, of course, no research substitute for old-fashioned, thorough, dissection technique, and more modern techniques usually are of little value unless critically integrated with it. Failings in this field also derive to a great extent from inadequate use of illustrations, especially of realistic representations of anatomical structures, for which there usually can be no adequate verbal substitute. In the literature, especially in major taxonomic works, the pictorial anatomical data are generally very crude or severely over-diagrammatic. On the other hand, in some significant publications, exceptionally neat or artistic renderings tend to lend undue credence to drawings which are scientifically deficient or seriously in error.

The higher Basommatophora, in general, are notoriously difficult to study and describe morphologically. The nature of the tissues of certain of their organs presents special difficulties in dissection and in sectioning. The radula and shell have optical qualities which make study of their critical microscopic details difficult, and they must be specially prepared for such study by methods that can be difficult and time-consuming. These problems are greatly compounded in studies intended to clarify the specific taxonomic characters of the snails. In such studies observations need to be made on very extensive series of specimens, as a rule, if valid results are to be obtained. This is necessitated partly because one commonly must deal with many forms which may be ill-defined species or mere variants of highly polymorphic species. Entering importantly into consideration here are the problems of distinguishing adult specimens from juveniles, and of defining size-differences between the species. Authors generally have underplayed this consideration. On maturing sexually the snails do not develop clear-cut external

characteristics that mark them as adults, and the limit of size to which they grow tends to be indefinite. On general external examination of population series, one acquires the impression that among such snails maturity is reached at a rather indefinite size. In a given population it would appear that, typically, some individuals mature at a much smaller size than others, and that other individuals do not mature until they have grown considerably beyond the size at which most of the population becomes adult. It also appears to be a general rule that different populations of a species tend to mature at different sizes, that some populations tend to be dwarfed, and that others tend toward giantism. It is probable also that each population tends to have a different radular tooth-formula since published knowledge indicates that the radula may grow, and show an increasing tooth-count, as long as the snail continues to grow. At the same time each population tends to have distinctive conchological characteristics. Adding to the morphological complexities is variation in general individual shell-form, and apparently in tooth counts, and occurrence of rather common radular and conchological anomalies. Probably similar interpopulation and intrapopulation variation occurs in the soft parts of the animal, especially in the reproductive organs, but this is difficult to prove because of possible, probable, or known effects produced by organ-functions, by preservation, and by factors relating to the individual health of the snails. In this problem, trematode infections commonly are involved, as probably are nutritional, stunting, and aging factors. It seems evident that ecophenotypy plays a role generally in the microgeographic variation of such snails, and that microenvironmental factors might relate importantly to variation within populations. It is very possible, however, that variation within these snails is greatly dependent on a marked, general, genetic heterogeneity. The species, as a rule, are made up of isolated and semi-isolated populations, and it may be that many of the populations largely originate from isolated single snails as pure genetic lines, which in time become interbred to very varying degrees with other pure or heterozygous lines. The species-problem then is much involved with, and greatly complicated by, the hermaphroditic nature of such snails, and questions about their ability to self- and cross-fertilize.

As a result of the situation outlined above, the morphological, phenotypic picture presented at the species level in nature by major groups of Limnophila appears to be chaotic. This circumstance is reflected in published taxonomies, as is to be expected, and in the fact that a great many, mostly dubious or invalid species of Limnophila have been described. In the Lymnaeidae alone, over 1000 specific and infraspecific names have been applied, although only 40 or so species may actually exist (Hubendick, 1951). Most of the nominal forms of Limnophila have been described very sketchily on shells alone and have never been reinvestigated. While we should call for much more extensive research to clarify relationships between such snails, we must realize that "correct," completely consistent, and truly adequate taxonomies for such snails probably can never be realized. In this circumstance it is important to make proper allowance for the fact that attempts to fit the species into neat and rigid nomenclatorial schemes may conflict with essential evolutionary and phylogenetic considerations, as I have found to be the case in the study of lymnaeids.

The lymnaeid described here represents a particular form which has been best known as *Stagnicola emarginata angulata* (Sowerby), but also by the prior name *S. e. serrata* (Haldeman). I have used the latter name in previous publications. I studied this form in connection with an extensive investigation of the comparative anatomy of many lymnaeid species or forms from various parts of the world. The studied snails represented all of the species-groups (and monotypic

"groups") which have been known by subgeneric or generic names. That study has continued for many years to the present, and in that time I unavoidably have accumulated reasons for abandoning the taxonomic system of F. C. Baker (1911, 1928) to which I attempted to adhere in the past. I find it quite necessary to reject all lymnaeid genera, except *Lymnaea*, and I have come to the tentative conclusion that practically all of the nearly 60 species of North American *"Stagnicola* s.s." recognized by F. C. Baker ought to be taxonomically united under the name *Lymnaea catascopium* Say. In this view, this species includes snails of very extreme gross body form like *"Stagnicola emarginata mighelsi"* Binney and *"S. exilis"* Lea. I also have many reasons for believing that *L. catascopium* is especially "highly" evolved, and here I propose the expression "advanced stagnicoline lymnaeid" to express this concept. Those reasons are largely dependent on data which are pictorially given here. My research results, in connection with published data of a very few authors (H. B. Baker, 1925; Jackiewicz, 1959; and Hubendick, 1951), have revealed a clear evolutionary connection of stagnicoline snails with the dominant group of old world lymnaeids which have been known under the generic name *Radix*, and which I must consider to be especially primitive. I refer to these as "radicine," following usage of Dwight W. Taylor (Arizona State University) in personal communications. In the Old World, at least 2 species which conchologically conform, more or less, to what is widely known as *Stagnicola palustris* Müller 1774, fall between the radicines and the advanced stagnicolines on internal anatomical features. They are "primitive stagnicolines." *"Stagnicola atkaensis"* Dall, which is limited to Alaska and adjacent territories, has primitive stagnicoline features, as does the circumboreal *Lymnaea stagnalis* Linnaeus, which heretofore has been the anatomically best-known lymnaeid, and which perhaps has been the biologically best-known basommatophoran. The relationships discovered show that shell-form can be extremely misleading in regard to relationships of species within the family. One European species which has an *"S. palustris*-type" shell is fully radicine in its anatomy, or nearly so. No one seems to know exactly what conchological form characterizes *L. palustris*, and I cannot be entirely certain that I have actually dissected that species in studying European forms. While my studies indicate that it is very likely that *L. palustris* and *L. catascopium* are very divergent species, the remote possibility remains that they yet may prove to be synonymous, in which case the former name, by priority, would have to be applied to the species described in this paper. Additionally, I have found that the limpet-like American snails commonly assigned to the genus *Lanx* and the subfamily Lancinae are with no serious doubt more closely related to *L. catascopium* than to the primitive stagnicolines. The group evidently evolved from *L. catascopium*, or a very closely related species, and has diverged but little in essential characters. On this viewpoint, the limpet-like lymnaeids are more closely related to some species of *"Stagnicola"* than are some species of *"Stagnicola"* to each other, and therefore I must reject the taxa Lancinae and *Lanx*. I also have evidence that leaves no doubt that *"Acella" haldemani* Binney, as well as one or more South American lymnaeid species, and most of the Hawaiian species, are advanced stagnicoline in character. Present evidence strongly indicates that the primitive stagnicolines are now largely confined to Eurasia, but that the advanced stagnicolines evolved from them in North America. A lymnaeid recently discovered in Poland, and described as a new species (*Lymnaea occulta* Jackiewicz, 1959), undoubtedly is of advanced stagnicoline character; one may suspect that it is an American species (*L. caperata* Say?) introduced into Europe.

While the preceding taxonomic-phylogenetic views cannot be considered at length here, I have previously published a considerable amount of data which

supports these views. Those data, however, were given in a taxonomic context which I now consider outmoded and ill-advised, while critical data I have obtained more recently, have as yet not been published. Data essential to these views have been published by authors (H. B. Baker, 1925; Jackiewicz, 1959; and Hubendick, 1951). However, the implications of those data for the present considerations were mostly not touched on by those authors, and in the last work cited the information is scattered in an elaborate context developed on a thesis contradictory to that proposed here. The information in the literature, including that which I have published earlier, can be assembled and collated only with considerable difficulty, and must be carefully compared with the illustrations given in this publication in order to understand adequately the grounds for the contentions I make here. Unfortunately there are certain probable to definite, misleading oversights and errors in the works just cited, which I cannot discuss at this time. Of special concern is a published description, for "*Lanx*" (H. B. Baker, 1925), of the prostatic tract, which supposedly differs considerably from that of typical lymnaeids. My studies have revealed that in at least one species of the "genus" that tract in all parts is like that figured here for *Lymnaea catascopium*. If what I consider to be *L. catascopium* actually constitutes many species, then it must be said that those species are so exceedingly uniform in their anatomy that a reasonably certain demonstration of the differences between them will require extraordinary efforts, greater than the extraordinary efforts I can claim to have made to that end.

It has been held that there is so little fundamental morphological diversity among the species of Lymnaeidae that we cannot hope ever to discover reasonably definite phylogenetic and zoogeographic relationships within the family (Hubendick, 1951). It is true that lymnaeids are relatively uniform as a family, in comparison with the ancylids and planorbids, but the present work proves that this contention has been seriously exaggerated. The pictorial information given here demonstrates that the reproductive anatomy of *Lymnaea catascopium* and its near allies is considerably more elaborate than has been supposed. Other lymnaeids, as a whole, diverge considerably from these advanced species in being relatively simple in characters of their reproductive system. One complication, the multiple folding of the prostate, apparently developed in radicine lymnaeids which gave rise to the stagnicolines. The most primitive stagnicolines exhibit the extreme development of this condition, but in the higher species the prostate has reverted to the unifolded condition which is characteristic of lymnaeids generally, and which is represented in figures given here.

Three major anatomical structures which are of fundamental importance to questions about evolution and zoogeography in the Lymnaeidae are described here. These are referred to as the copulatory holdfast apparatus, the prostate pouch, and the uterine cecum. The latter structure is almost universal in lymnaeids, but is lacking in the most primitive stagnicoline snails, while the former structures have been developed fully only within the higher stagnicoline evolutionary line. The outstanding evolutionary change during the rise of the higher lymnaeids has involved modifications of the penis and vagina, which in mutual adaptation to each other have produced the copulatory holdfast mechanism. The primary evolutionary step leading to this was the extreme reduction in the primitive stagnicolines of the ancestral long, simple, radicine penis. An essential part of the holdfast apparatus, here called the penial knot, was first clearly identified by F. C. Baker (1928), who also gave vague evidence of the existence of the prostate pouch and uterine cecum in a form of *Lymnaea catascopium*, in a figure in one of the first of his many publications on lymnaeids (1900). H. B. Baker (1925) first

clearly described the stagnicoline prostate pouch in a species of "*Lanx*," and Jackiewicz (1959) was the first to give a clear figure of that pouch. My studies confirm the contention of F. C. Baker (1911, 1928) that bicuspid lateral teeth are characteristic of the American "stagnicolas." Certain other species have similar teeth (example: *L. bulimoides* Lea), but in the advanced lymnaeids the bicuspid teeth are especially robust and constant in character.

So many lymnaeid anatomical features are newly described and figured here, or clarified adequately for the first time, that a list of them would be quite lengthy, and would include reference to much data to be referred to hereafter. It is not entirely practical to point out everything that is or is not new knowledge here, for this and related reasons. On working out the morphology of the reproductive and venous systems to relative completion in critical respects, heretofore unknown or unclear implications came to light in regard to physiological function, and this has made it possible to propose for the first time relatively complete, although partly theoretical, schemes for reproductive processes and the venous circulation. These schemes are given some special emphasis in the following account, because they are of such basic biological significance, and because they are importantly involved in basic problems concerning the homology and proper terminology of organs. The reproductive processes are emphasized particularly because they may alter significantly the morphology of organs which are very important in anatomical comparisons in taxonomic work. Neglect of this matter can result in serious taxonomic misconceptions.

Included here are data which relate to the ontogeny, seasonal variation, life cycle, population dynamics, and parasitic infections of the described snail. These biological phenomena have significant implications for the morphological definitions of species which show the kind of biogenetic potentialities that snails such as lymnaeids exhibit. In captions for the figures given in this paper, I have included much verbal data which are mainly meant to call attention to factors which must be considered in application of the given morphological data in comparative work, and to indicate the need for special research on the role of such factors in the scientific problems involved.

The pictorial account given here is based almost entirely on a single lake population of *Lymnaea catascopium* in Michigan, U.S.A. All but one of the given figures were made from snails of that population. This population was considered by F. C. Baker (1911) in his definition of the "*angulata* race." It was intended that this population, representing a restricted gene pool having limited phenotypic potentialities, be studied as thoroughly as possible biologically as a preliminary to comparing many species. The population was studied for more than a year, during which extensive field observations were made, mostly at monthly intervals. Conchometic and anatomical analysis of population samples taken at those intervals were made also, and snails descended from that population were reared in aquaria so that growth phenomena could be directly observed. During that study numerous anatomical and field observations were made on a great many nominal species of "*Stagnicola*," and on other lymnaeids. Also, many museum shell-series were examined. Detailed, although not complete, results of these studies, including extensive anatomical descriptions and the figures given here, have been available for many years in the form of a booklet printed from microfilm made of a ponderous doctoral thesis (Walter, 1961). I have also given data from additional lymnaeid research, but without illustrations, in small published works (Walter, 1959; and Taylor, Walter & Burch, 1963). The more recent of these papers gives a detailed textual description of the reproductive system of an advanced stagnicoline lymnaeid, *L. caperata* Say, along with critical comparative

data on other species. The works of mine just cited employ a taxonomy and an anatomical terminology which I have greatly revised for the purposes of the present publication. I have published further anatomical and conchological information which pertains in small part directly to Lymnaeidae, but which mainly concern planorbid intermediate hosts of human schistosomiasis, and broader comparative-taxonomic problems in Limnophila (Walter, 1962, 1963). In the present work I have had to pass over microconchological considerations, even though they may have considerable importance in lymnaeid comparative morphology. I have given special attention to microconchology in Basommatophora in one of my papers (Walter, 1962). A brief account of my views on relationships among the world's lymnaeids is now in press.

I cannot consider here the literature on Lymnaeidae and other Basommatophora at length, but in the Bibliography I present a list of pertinent references. The list is relatively extensive in respect to papers that concern lymnaeid taxonomy, morphology and anatomical function, and it includes titles that I consider to be of exceptional significance in respect to the broader morphological-taxonomic problem in the Basommatophora. Certain titles are given to provide some representation of significantly related literature, such as that dealing with anatomical technique, and with paleontological considerations (Taylor, 1966). The more modern literature is largely represented, and works having extensive bibliographies which will serve as a guide to the older literature are included. Taxonomic monographs of Hubendick (1951) and F. C. Baker (1911, 1928) together, provide a detailed worldwide view of the taxonomic problem in Lymnaeidae. F. C. Baker published a great many taxonomic papers on lymnaeids over the years, especially on forms of *Lymnaea catascopium;* his monographs have had a great influence on workers in this field, and his taxonomic views on certain species of *"Stagnicola"* shifted significantly toward the end of his career. Since these matters relate especially to the rather revolutionary taxonomic-phylogenetic views I have given here, I have listed among the references many of his lymnaeid contributions, especially those which concern stagnicoline species. Also listed as references are several monographic publications on Planorbidae, containing extensive information on anatomy, authored by F. C. Baker (1949) and Hubendick (1955). In the current description of morphology and functions I make reference to a number of specific ideas which I was not able to account for personally, and which I obtained from the publications of others. The source of most of these ideas may be accounted for as follows: sperm-ingestion (Fretter & Graham, 1962); structure of the wall of the prostate (Hubendick, 1947; H. B. Baker, 1925); the role of a mucoid secretion in respiratory inspiration (Cheatum, 1934); "lymphatic" tissue near the kidney (Taylor, 1894-1900); sperm-packets carried by the seminal gutter (Bretschneider, 1948a, b), and neurosecretion (Lever, deVries & Jager, 1965). Also, a considerable number of ideas given about the function and nature of parts of the digestive tract and associated structures are derived from the work of Carriker (1946a and other papers). The compendious work of Fretter & Graham just cited, which is on prosobranch snails, is a very important source for comparative information which can shed light on fundamental anatomical, functional, physiological and biochemical questions regarding Basommatophora. Crofts (1929), in a work on a prosobranch snail, has given information which may relate significantly to the gland field of the lung described here. Many of the structural and functional aspects of lymnaeid or basommatophoran morphology, which I elucidate here for *L. catascopium*, previously have been accounted for, to some extent, by various authors for other basommatophoran species. I have given as many titles pertinent to this as seems practical in the reference list. Special attention deserves to be called to works of certain authors, which are

outstanding examples of the unparalleled importance of excellence in pictorial demonstrations of morphological facts. These are works by Carriker (1943, 1946a, b), Larambergue (1939), Demian (1960, 1962), H. B. Baker (1925), Jackiewicz (1959), and Paraense & Deslandes (especially 1959, among many papers on Planorbidae).

Anatomical terminology has presented a great problem in preparing this work; that which I have applied here is in considerable part of my own making, yet it is by no means satisfactory to me. This publication, in fact, is designed to help establish grounds for eventual development of a satisfactory terminology. Because so much described here has not been known previously in any snail, there were no terms available in the literature for a wide variety of structures, representing most of the organ systems. I also found much terminology in the literature to be ill-advised, for many reasons, and have avoided such terminology in this work. I have even avoided using the words "pallial" or "mantle" in the generalized traditional way for a region of the body and for organs related thereto. The word has been applied too loosely and vaguely by many authors, at least in respect to the "pulmonate" basommatophorans, for which the question of just what are the topographical "pallial" limits can be a matter for argument. In particular, one may question whether the "mantle collar" is associated with true pallial tissue (the epithelium which constitutes pallium or mantle *per se*). In my descriptions I have tried to avoid unnecessary use of new technical terms and terms of authors which have a scientific appearance, rather than scientific merit. A very large part of the terms used are adapted from the elaborate terminology system provided in the major morphological paper of Carriker (1946a) on the primitive stagnicoline snail, *Lymnaea stagnalis*. This paper, among others of Carriker (as cited earlier) and Carriker & Bilstad (1946) on this snail, primarily concerns the functional anatomy of the digestive system, but it also deals extensively with the nervous and circulatory systems. For these several systems, these authors not only account for gross anatomical structures, but to a great extent for microanatomical details and histology. That work may represent the most admirable, and most comprehensive and detailed study ever done on a basommatophoran snail. My own research on the same and related species attests to the high degree of accuracy of that work. As is to be expected, *L. stagnalis* and *L. catascopium* are essentially identical in the anatomy of the organ systems those authors especially dealt with. Accordingly, the above cited publications of those authors can serve as an explanatory text for much of what I present here pictorially. I have avoided verbal exposition of my data where it would only be a repetition of what they account for at great length.

On the taxonomic view I adopt, *L. catascopium* is a species which is highly polymorphic in superficial characters and which ranges from coast to coast across North America, from north of the Arctic Circle in Alaska and Canada, south to southern California, to New Mexico, to southern Ohio and to New Jersey. Over much of that range this species is very abundant in diverse habitats, ranging from ditches, ponds and marshes to strongly flowing rivers, and to open situations in large lakes. The anatomical uniformity of the species is particularly significant in view of this situation. About 20 microgeographic forms of the species, primarily found in lakes, but also in rivers, have been supposed to belong to "races" or varieties of *"Stagnicola emarginata"* and to species especially allied to them. These forms are largely endemic to the Great Lakes Region and central Canada. The lake forms, especially those to which the trinomial name *angulata* has been applied, have been of some economic and public health concern as vectors of "swimmers' itch" at tourist resorts. In this con-

nection, Cort (1950) and his colleagues have published several papers on the life cycle of *"angulata"* and on its biological relationships to the life cycles of trematodes. There are quite significant differences between my account of the life cycle of *"angulata"* and that of these authors. In considering the wide geographic range and the diverse environments which *L. catascopium* occupies, one may note that its life cycle must vary drastically from that described here, depending on local circumstances, and that its food habits may vary similarly. The snail pictorially described here lives in a great and dense permanent colony in a very large shallow lake (Houghton Lake, Michigan, U.S.A.), on a bottom of rather coarse sand. The snails regularly ingest this sand in large quantities, and in the process they consume much psammon, especially quantities of diatoms, and a crustose blue-green alga having a deep yellow color in its mucilaginous sheath. Further information about the biology of *"angulata"* may be found in the combined works of F. C. Baker (1900, 1911, 1928, among other publications), Cheatum (1934), Hubendick (1951), and a few other authors.

This work would not have been possible without the help given me in way of professional or personal support by Dr. J. B. Burch, Dr. Henry van der Schalie, Dr. Arthur H. Clarke, Jr., Dr. J. Allen Scott, Dr. Vera King Farris, Mrs. Herma Van Bomel, Mrs. Arthur Honeyman, Mrs. Barbara Langford, Mrs. Elizabeth Smith and Miss Mercedes Weber. Dr. Leonard Allison, and Messrs. Lloyd Goine, Frank Hewitt and Matt Lagerburg also gave assistance which aided in this research. I express my appreciation to all these persons.

METHODOLOGICAL INFORMATION RELATING TO THE FIGURES

Much of the pictorial information given here cannot be applied or confirmed readily in comparative research without due consideration to the varied means used to make the observations on which the illustrations are based. All of the drawings were made from dissections using a stereoscopic dissecting microscope which provided magnifications up to X60. All figured sections of structures were made by slicing organs with a microscalpel, as they lay in a dissecting dish. Such thick sections were observed by intensely concentrated, reflected light of a high intensity microscope lamp. A limited number of microtome serial sections were studied to confirm or clarify some structural detail revealed by dissection. All anatomical observations were made with the preparations completed immersed in fluid. This work required 2 pairs of fine-pointed watchmakers' forceps, which were often used simultaneously; other tools consisted of small dissecting needles and clamps, made from "minuten nadeln." The needles were largely used as microprobes. In order to make observations of minute structures, it was necessary to pin and clamp them to the dissecting dish. Specimens collected in nearly every month of the year and of all sizes, were dissected. Most drawings were made from expanded specimens which had been "narcotized" or "relaxed" with solutions of sodium nembutal or other chemical agents, prior to preservation. Such specimens were rapidly killed with Bouin's fluid to preserve them in an optimally expanded condition. Following fixation, the specimens were stored in a variety of commonly used preservatives, such as hydrated ethyl alcohol, formalin, etc. Many specimens were dissected alive in a "*Lymnaea* physiological salt solution", developed and described by Carriker (1946a). A variety of liquids, including water and ethyl alcohol, served as dissecting fluids for preserved specimens. Determination of the correct features of certain anatomical structures required numerous dissections, and repeated preparations were made to confirm those features, and to determine their degree of constancy. In such efforts it was necessary to acquire a great familiarity with the tissues in various states of preservation, and in the living state. Certain features could be determined only in living, underpreserved, or very recently preserved specimens, and certain other features could be determined only in snails which had been overpreserved, or preserved for lengthy periods. Almost any modification of preservation methods resulted in both advantageous and disadvantageous effects. "Narcotization" produces some unfavorable effects, which were circumvented by drowning specimens instead. Specimens in all states of contraction were dissected, to observe effects of contraction. Deliberately varying the chemical concentration of the dissecting fluid in which a given specimen was immersed shed light on the effects of preservation on the organs. The shrinking and swelling of tissues can be manipulated readily in this way. Staining the preparations in almost any way with almost any dye aided in making observations. Study of very darkly stained organs and entire specimens by intense reflected light revealed a great deal about the distribution of cilia. Thoroughly bleaching organs and whole snails aided importantly in the determination of various anatomical details, as did clearing specimens to various degrees. In such specimens, relatively crude methods of injecting colored fluids revealed important features of venous circulatory patterns. Determination of such patterns and other anatomical details partly depended on mounting various parts of the body on glass, and studying them by transmitted light. Radulae were extracted by the rapid method of heating the buccal structures in concentrated potassium hydroxide. The teeth were studied and photographed while temporarily mounted in water. Radular photographs were

made with a single-lens reflex camera mounted on a dissecting microscope.

In effect, the drawings are almost all careful tracings of observed features. Accuracy was assured by viewing each preparation through the grid of a Whipple disc set in the ocular of the microscope, and transferring the image with great care to grid-ruled paper, square by square. As a result, the figures mostly represent particular specimens and their individualistic features. Many of the drawings were made from a particular individual of large adult size, having a shell length of 24 mm. Some drawings are composite, in which features of several specimens were combined, while a few others are based on measurements and generalizations derived from the study of hundreds of dissections. The given drawings are the winnowings from a vastly larger number made at the microscope.

In the figures, stippling has been used sparingly for shading, so that it could be employed to indicate granular pigmentation, or in cases, cut ends of fibers in cross-section. To make it possible to show the maximum number of anatomical features with a minimum number of drawings, structures in certain illustrations were selectively eliminated or distorted, or they are represented as transparent; only during dissection can one fully appreciate what was intended in such cases. A number given in parentheses below a drawing is meant to indicate the shell-length, in millimeters, of the particular specimen represented by that drawing. Except where indicated otherwise in particular cases, the figures represent adult snails.

All but one of the figures (Fig. 91) are based on the Houghton Lake population of the *"angulata"* form of *Lymnaea catascopium*. For practical purposes, one may utilize several papers by Carriker, and Carriker & Bilstad, listed among the references, as textual matter on the function, microanatomy, and histology of much of the alimentary, circulatory and nervous anatomy figured here.

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LIST OF ABBREVIATIONS

a.	subsutural angle of body whorl
an.	position of anus (hidden)
ant.	anterior
ar.	artery
b.	body
cl.	ciliated
comm.	commissure
conn.	connective
d.	duct
dils.	dilators
do.	dorsal
f.	fold
fi.	fibrous
fd.	field
flex.	flexor
ga.	ganglion
gen.	genital
gl.	gland
gl. fd.	position of gland field (hidden)
gr.	groove
h.	hepatic
herm.	hermaphroditic
l.	left
lat.	lateral
levs.	levators
m.	muscle
m. t. a.	muscle tract of the angle
med.	median
mi.	minor
mj.	major
nv.	nerve
o.	opening
od.	odontophoral
os.	position of osphradium (hidden)
ov.	oviducal
p.	passage
po.	pore
pc.	procurrent
post.	posterior
protr.	protractor
protrs.	protractors
pulm.	pulmonary
pulm. vlv.	position of pulmonary valve (hidden)
py.	pyloric
r.	right
rad.	radular
ren. po.	position of renal pore (hidden)
retr.	retractor
rc.	retrocurrent
s.	strip
sp.	spongy
st.	stratum
susp.	suspensor
t.	tract
tens.	tensor
v.	vestibular
v. o.	opening of hepatic duct into pyloric vestibule
vg.	ventrogastric
vlv.	valve
vn.	ventral
vp.	ventropyloric
vv.	ventrovisceral
w.	whorl

LEGENDS TO FIGURES

FIGURE 1. Shells of *Lymnaea catascopium* Say, from the population on which the succeeding anatomical figures are based. The series of shells, as figured, is recognizable as belonging to the variant unique to Houghton Lake, Roscommon County, Michigan, U. S. A. On gross conchological features this population in the past has been included in a supposed race, best known as *Stagnicola emarginata angulata* (Sowerby), or as *S. e. serrata* (Haldeman). In this figure the shells are arranged to illustrate some features of population dynamics revealed by conchological and anatomical analysis of large semi-quantitative samples taken in most months over a 17-month period. All shells but one are shown in ventral (apertural) view. The number of whorls of adult shells was about 5 1/2 on the average, and about 6, at the extreme. The sculpture is stagnicoline, in being rather coarse. Photographs by J. B. Burch.

Rows A to D: Shells representing a class of snails of "aged" or weathered aspect, which entirely made up the very large population when it was first sampled extensively, on its emergence from the winter of 1956-57. From about 2,000 specimens collected in all seasons, the shells shown were selected to illustrate both the more common and the more extreme variations in various characters. The first shell (Row A), is fairly typical, but it was the largest found, and it was longer by about 1/3 than the average adult shell. The character of the subseries in Rows B to D, including the mean and range of size (length), closely corresponds to that of the whole population at the time of the first sampling, in April. It appears that at that time the population was largely made up of 2 generations, believed to have arisen successively in 1955 and 1956. This is an inference made largely from data on 2 generations that appeared successively in 1957 and the next year. After producing prodigious numbers of eggs in a period which largely fell in April (1957), snails of the weathered class continued to be very abundant, at least into the following November, and considerable numbers survived at least until the second week of May 1958, when the sampling program ceased. Those surviving to the latter time had lived through at least 2 winters; possibly many of them, and probably at least a few, had overwintered thrice, and, it is suspected that a few individuals may then have been survivors of 4 winters. It seems that special factors existing prior to the study, and connected with the aged appearance of this class, had levelled out all definite differences in size and in related morphological characters that once existed between the generations. Even extensive conchometric analysis of samples taken in all seasons failed to demonstrate size classes among the weathered snails.

As with other lymnaeids, juvenility or maturity is expressed in the shells in this population in indefinite or inconsistent features which relate to shell size only in a general way. Over a rather broad range of sizes, mature and immature specimens can only be separated from each other with certainty on relatively direct evidence of their individual reproductive status, which morphologically relates most clearly to development of the albumen gland and coloration of the gonad (cf. Figs. 51-54). Study of the reproductive system in this population showed that in approximate terms, the snails commonly became subadult on reaching 11 mm in shell length, and reached adulthood on becoming 16 mm long. Maturation seems to have been delayed or accelerated in many individuals. All specimens with shells 20 mm and longer may have been mature, but even this is not certain. Throughout the first year of sampling, the aged snail-class changed little in size. Apparently, growth among the snails had

continually balanced out mortality-loss of larger individuals, while a growth-lag among many smaller individuals tended to keep the lower range in size extended. In samples from all seasons, the mean shell length stayed within the limits of 18 mm to 22 mm, and specimens with shells 16 mm to 23 mm long were always present. Larger snails with shells up to 26 mm long, appeared sparingly in most months, but were common in the second May of the program. Rarely, slightly larger shells were found. Weathered specimens of sub-adult size, only about 13 mm long, appeared in moderate numbers in the initial sampling; it is believed that they and the 6 smallest specimens shown (Rows C, D) were stunted. Some of them were examined for their gonadal condition, which appeared to reflect aging (cf. Fig. 53). Apparently, after overwintering, few if any such individuals grew significantly, and, slowly dying out, they disappeared several months before the onset of the next winter.

Most or all shells of the population possessed a number of axial varices (calluses), each of which marked the lip of the shell when it was in some smaller and younger stages of growth. In given shells, some varices were sharply defined and distantly spaced from others, while other varices were diffuse and vague, and crowded together, or mergent. Only ill-defined varices were detected in some shells, even large ones. Usually at least one strong varix was detected high on the spire, but it was commonly obscured by erosion; this varix set off what was once a small juvenile shell. Many measurements based on the positions of the more marked varices showed that they had tended strongly to develop when the shell reached certain approximate sizes, even though variation among individuals was such that varical development had occurred at any size. A strong lip-varix had formed on the shells generally, as they grew from about 1 to 5 mm in length, and when they reached successive lengths, on the rough average, of 8, 11, 16 and 22 mm. At least one additional varix tended to develop in snails more than 25 mm in length.

In early July most shells had firm, thickened lips and all snails in September, November and December showed that condition. In late April and May, and in early August and October, however, the outer lip of the shells of much of the population was very thin and fragile. The fragile material was an increment to the shell, extending from a previously varically thickened lip. The increment formed a narrow border on that lip in many of the snails in April, and in nearly all of them in October. In May and August, the fragile growth occurred in generally extensive but variable amounts, throughout much of the adult population, especially in the latter month, when it made up a large part of the body whorl of some shells. Observations on growth of individually "tagged" snails in the laboratory showed that such an increment is produced in one phase of rapid, sustained growth, which may show poorly defined subphases. Such a phase is followed by an interphase in which growth ceases or is retarded and in which the fragile shell increment is reinforced by a general thickening, and the addition of a varix to its lip-edge. It then seems evident that the field population experienced 2 major "waves" of rapid growth during the year, one in the spring and one in the summer, and underwent a lesser wave in the fall. Features of growth-stages suggested that there had been waves within waves also, and that some snails had grown relatively continuously during most of their life. When snails are raised in aquaria, in which they are subject to mutual crowding and related special limiting factors, it seems that their growth depends considerably on mutual influences among them. The field population was found to have a very high density throughout the year, and accordingly, similar influences might have had effects in the natural habitat, to a considerable degree, as the study of field

1

samples indicated. Growth of an aquarium population tends to occur with successive waves sweeping through the population. A growth wave results when growth phases of some snails become roughly synchronized. As the snails involved in the wave enter a resting interphase one by one, a number of other snails enter growth phases and create a similar wave, which ends similarly; then, snails of the preceding wave, or other snails, participate in another wave. It seems that each wave is triggered by cessation of a preceding wave, and that each wave results in temporary inhibition of growth of the larger part of the population. When a brood is hatched in an aquarium it seems that a few snails quickly gain a growth advantage, and become "favored" to mature first and grow to the largest sizes. They seem to dominate the growth pattern of the population, by creating repeated "leading waves," which tend to inhibit the growth of the remainder of the population. Similarly, other "wave-groups" of snails seem to influence others within a population heirachy of growth-dominance. It is thought that the more favorable are macro-environmental conditions for growth the less this system operates, and that under less favorable circumstances micro-environmental factors influence the role of segments of the population in it to an important degree. Evidently, this system tends to result in stunting at lower levels of the heirarchy, and thereby suppresses a great number of snails of the lowest level, which are destined to die off slowly without growing much beyond hatching size. Stunting especially appeared to relate to severe limitation of growth of later shell stages, and, as is detectable in the figure, with unusual thickening at the lip of the shell.

Trematode infections were observed commonly in specimens of adult size; perhaps they affected shell characters or size of the animal but this was not evident. Practically all snails of the weathered class carried in their gonads an unidentified parasite (an encysted mite? - cf. Fig. 52), which produced no known morphological effects. This weathered class appeared to be aged because nearly every one of the shells showed some erosion, especially at the tip of the spire, some encrustation with a blue-green alga, and discoloration relating to the latter (the figured shells have been cleaned).

All but a small percentage of the shells had a true ground color of various shades of buff to brown, deep red apical whorls, and reddish varices. The last 4 shells in Row D are white, and lack all color traces, but are not "albino." Color of the shell or its lack was not related to color of the soft body.

Row E: These are shells of a generation which hatched in vast numbers in late May and June, 1957, as offspring of the weathered class discussed above. Their shells were about 1 mm long at hatching. In the following November, after great numbers had died out, numerous survivors obtained in field samples had attained an average shell length of about 13 mm, and shells of a very few had become 18 mm long. A sample taken the following mid-May (when a large new generation was hatching), showed that snails of this class had then reached a mean shell-length of about 15 mm. Few if any had grown beyond 18 mm. At that time, this generation made up about 3/5 of the near-adult and adult portion of the population. Although they were then about a year old, shells of the 1957 brood had a relatively clean, smooth, unaged appearance by which they could be distinguished from nearly any of equivalent size that belonged to their parental group; also, they tended to be more obese and less scalariform than the parental class. Two or 3 growth stages had become clearly established in most of the year-old shells. An apical thickened stage of a few whorls had appeared early in the growth of most. The last 2 shells in the row are entirely white; the remainder are variably colored like those of the older class, but are mostly lighter

and brighter in tone. Note that the columella is gyrate in earlier stages of the shell.

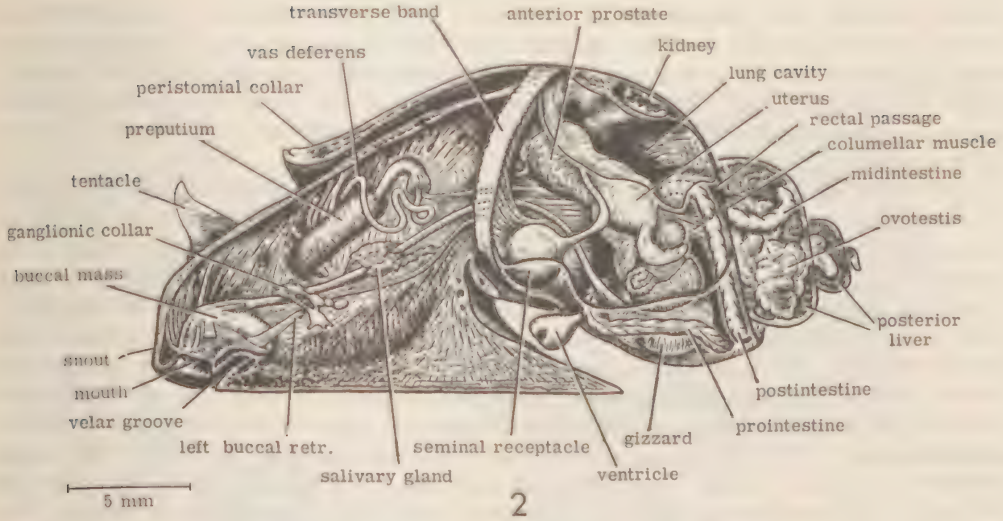
Row F: Shells of 3 specimens which were raised in aquaria to an age of about 1 year, from eggs laid in the laboratory. Two are typically colored and one is entirely white. The remaining shell is of the aged field class; it is oriented in side view to indicate the characteristic attitude in which the snail would carry it during locomotion.

FIGURE 2. The adult animal, with the shell removed, in the locomotory posture, showing its living proportions and contours in relationship to internal structure. The body is shown as if its walls were cut away to the left of the sagittal plane, so as to leave internal organs largely intact. Many smaller structures and obscuring tissues are omitted. The heart (with its auricle removed) is shown pulled out of its normal position (cf. Fig. 4). The heavy black line shown passing over the seminal receptacle indicates the left-hand boundary of a portion of the lung that has been removed. The genital complex under the lung is shown somewhat smaller than is normal in a healthy adult. The transverse band approximately marks a region of differentiation of the body into a cephalopedal (head-foot) mass and a visceral mass. Skirt-like, the peristomial collar embraces a cervical region, or neck, around which it forms a water-filled cavity. The integumentary epithelium lining that cavity, and the head-foot, is ciliated - mostly with ciliary tufts - while that of the outer collar wall and visceral mass is unciliated, and constitutes the pallium (mantle), at least in the latter region. The view reveals the 2 primary cavities of the body, the cephalopedal and visceral hemocoels, which are separated in life by a transverse membranous midbody ("cervical") septum (not shown) under the lung, where the esophagus and the duct of the seminal receptacle cross in the figure. Most of the shown organs lie in 2 major venous blood-pools which correspond to these cavities. The rectal passage is the primary venous outlet of the visceral hemocoel (cf. Figs. 5 and 50). The shown surfaces of the dorsal and lateral hemocoelic wall anterior to the transverse band are formed by contiguous and overlapping bands and sheets of muscle; valvular oval foramina (indicated as black ovals) between those muscles lead abruptly into well-formed venous canals (cf. Fig. 49) within a superficial subepithelial stratum of spongy tissue containing innumerable musculoconnective fibers. In lower lateral and anterior areas, larger oval foramina (note one near the anterior base of the preputium, the tentacular foramen), which serve as passageways for venous blood, arteries and nerves, lead into more massive beds of spongy-fibrous tissue. The cephalopedal hemocoel is floored by a yet more massive bed of similar tissue lying against the thickened epithelium of the sole of the foot. This bed is riddled with muscle fibers (indicated as fine short lines). Just above the latter stratum many separate well-spaced muscle strands pass transversely through the hemocoel. The epithelium of the sole contains innumerable closely packed vertical fibers; these are evidently modified cilia, which barely protrude on the sole's surface. Concentrations of gland cells lie on the epithelium of the sole at the anterior end of the foot: these cells undoubtedly provide the sole with its coat of slime. The rectal passage apparently is the primary pathway for trematode parasites in their migration from the visceral hemocoel to the body surface, when they are ready to leave the snail. In immature snails, the buccal mass and nerve collar are relatively large: and in very small, young snails they are relatively enormous.

FIGURE 3. The peristomial collar, and the adjacent roof of the lung, viewed from the right side, showing superficial muscular elements and topographic relationships of "pallial" structures. A bold to obsolete blackish pigment pattern, largely within the mantle epithelium, commonly obscures structures shown in the lung wall. Three heavy dashed lines partially indicate boundaries of the lung. Numerous muscle elements subjacent to the integumental epithelium are indicated by solid lines. More delicate, shorter lines indicate fine separate musculoid fibers, while stronger, more continuous lines represent relatively coarse, close-set strands and bands. Many spaced muscle bands deeper than these are indicated in a grey tone. The five features indicated by abbreviations lie under outward surfaces and are not actually visible in the given view. The anus opens at the juncture of the siphon and the collar. The osphradium is a small organ largely imbedded in the collar wall just in front of the "siphon" (cf. Fig. 38); it has a lumen which communicates with the water-filled space formed by the collar (the anus empties into the same space), and it presumably functions in sensing physical or chemical characteristics of matter in the environment. The renal pore lies on the inward surface of the lung wall, next to a D-shaped, grey-pigmented field of gland cells (heavily outlined in black; cf. Figs. 41 and 43). The gland field lies in the lateral lung wall directly over the pneumostome, a capacious respiratory opening (cf. Fig. 35). The siphon is suspended bag-like from the margins of the pneumostome, which it blocks when contracted. It functions in the intake and release of air (or water), during which the figured broad slot in it closes and opens widely in different functional stages. It is shown moderately extended. The gland field probably supplies it with a special thick slime which is necessary to its function. The pulmonary valve is on the floor of a small venous sinus having a thin musculomembranous roof overlain by "pallial" epithelium. That sinus lies among tissues which form the juncture of the lung wall, the transverse band, the collar, and the neck of the animal. The valve is of primary significance in the venous circulation of the body (cf. Figs. 49, 50). The ridge on the collar is a sharply elevated, flat-topped band of distinctive "cuticular" consistency, and it is formed on one of 2 lip-like shelves, separated by a groove, at the collar's margin.

FIGURE 4. The body whorl of the animal in left lateral view, with muscle elements and the margin of the lung indicated as in the preceding figure, and showing further "pallial" structures. The topographic relationship between the kidney, heart and lung is clarified further in Figs. 42, 43, 47 and 50. The deep diagonal muscle strands anterior to the kidney pass through a mass of large globular cells having bluish, viscous contents. The more dorsal portion of the kidney may be a conspicuous external landmark in life which appears as a bright cream- or yellow-colored structure. However, a conspicuous concentration of black pallial pigment often hides the color. Determination of the outlines of the organs shown depended partly on thorough bleaching of the tissues.

FIGURE 5. Musculature of the body, with a representation of the form of the animal when it is in locomotion. The visceral mass is shown swung to the right from its more typical position (as happens in life), in which it points somewhat to the left. The finer, shorter lines indicate the presence of innumerable fine separate muscular fibers next to the epithelium in the more dorsal cephalopedal areas, and which occur deeply as well as superficially elsewhere. Relatively massive muscle tracts and their offshoots are heavily outlined. Clear areas showing between these tracts represent muscular sheets and bands di-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columellar muscle
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ovotestis
ganglionic collar
buccal mass
posterior liver
snout
mouth
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prointestine
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seminal receptacle
gizzard
salivary gland
ventricle
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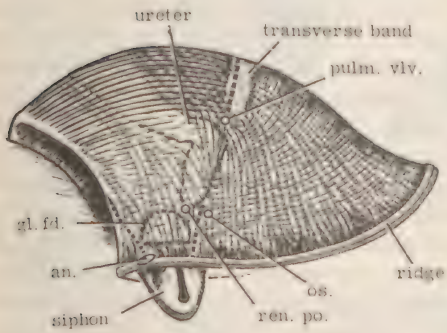
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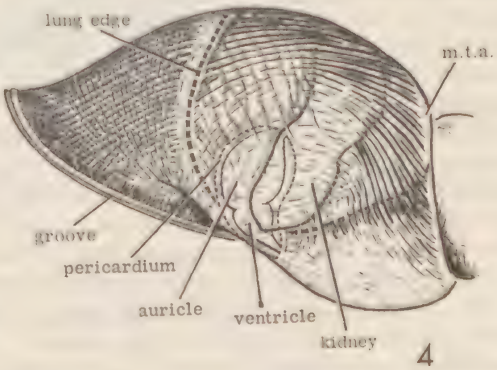
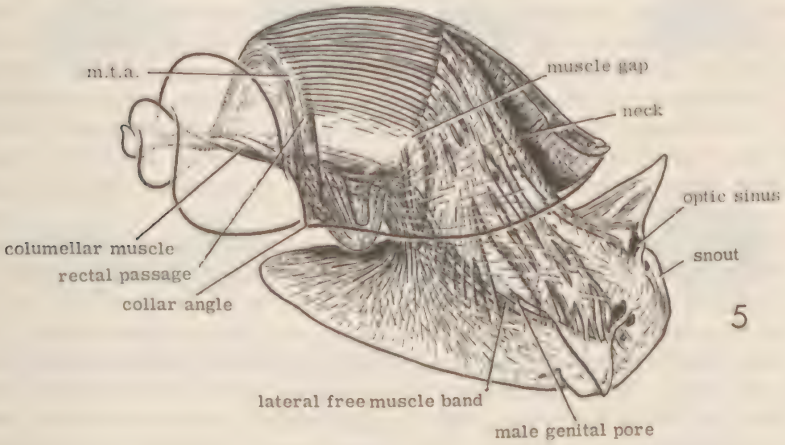
siphon
ren. po.

3


lung edge
m.t.a.
groove
pericardium
auricle
ventricle
kidney

4

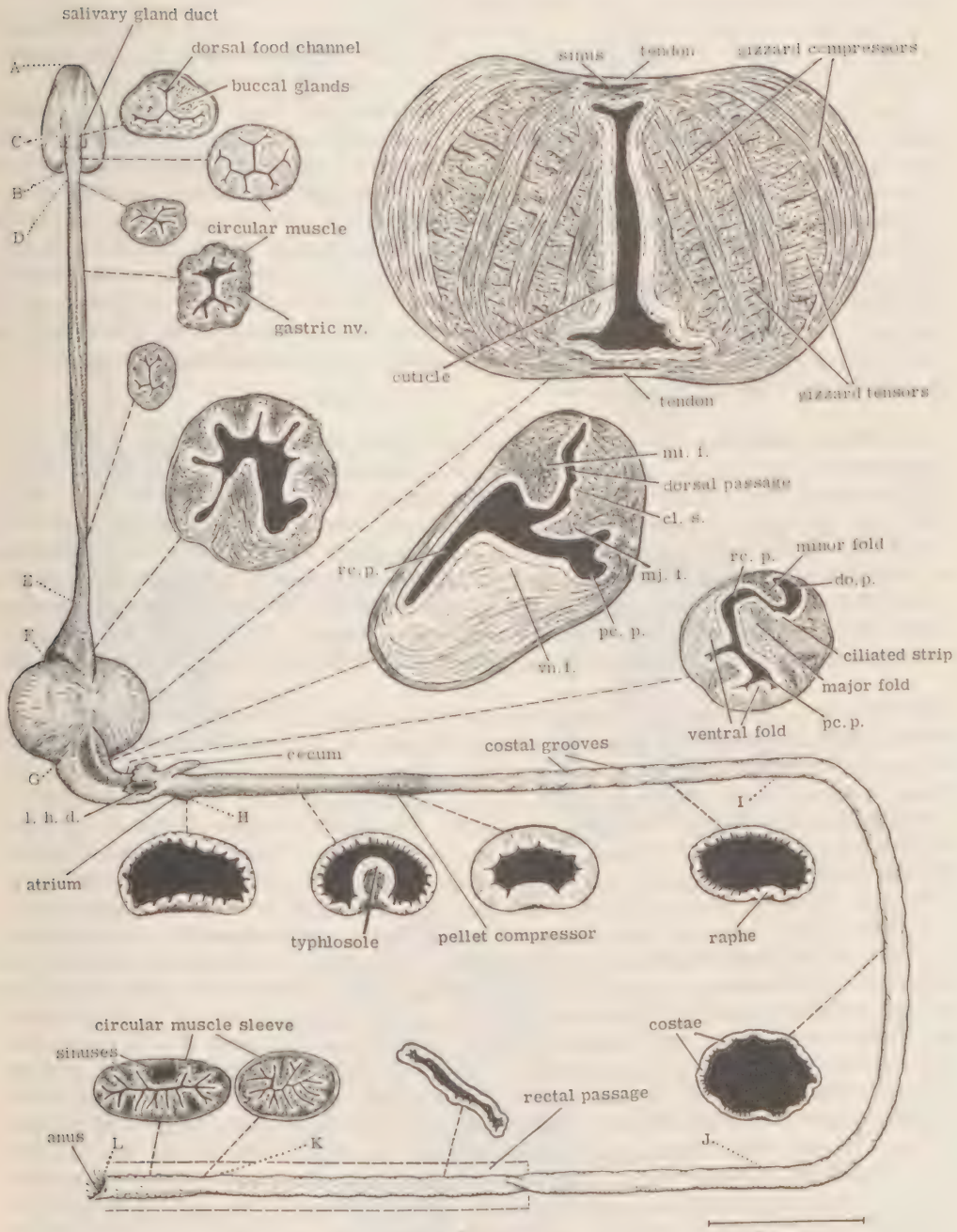

m.t.a.
muscle gap
neck
optic sinus
columellar muscle
snout
rectal passage
collar angle
lateral free muscle band
male genital pore

5

rectly roofing the hemocoel of the head-foot; black ovals represent venous valvular passageways leading outward through those areas. The diagrammed muscle bands of the lung roof are the suprarenal muscle bands indicated in Figs. 3, 4 and 42. The clear areas shown in the spire region represent the very thin musculomembranous body wall, which consists in part of a fused meshwork of fine fibers, and in part, of the pallium (epithelium).

The color of the body shows conspicuous individual variation, partly because of variation in the amount of black to sepia pigment which occurs as microscopic flecks on practically all bodily structures. In a small percentage of the population the flecks are almost entirely lacking. Generally, the head-foot mass, in gross external view, is dark purplish-grey to deep chocolate brown, but it varies to an intense clear yellow, and to a pale yellow-grey. The yellow color seems to stem from food consumed in the habitat. This color does not develop in lab-reared specimens. In life, the frontal region (cf. Fig. 34) shows blended red and black tones because the buccal mass (cf. Fig. 6) and the capitocerebral membrane (cf. Fig. 30) show through the body wall there. The red color of the gizzard (cf. Figs. 2 and 6) also shows through the body wall, and often through the shell, and thereby provides an important external topographic landmark. On the peristomial collar and the body regions posterior to it, dark pigment flecks, largely in the pallial epithelium, are concentrated to form a basic pattern which is bold in some individuals, but which is more or less obsolete in most of the snails. In well-pigmented individuals, the apical half of the spire whorls is duskily pigmented on the surface (and often stained with a blue-green color as well), but the anterior half is contrastingly pale. The surface of the roof of the lung is broadly blotched with black. Circular interruptions partly break up the surface pattern into a reticulum on the posterior region of the lung and on the spire. The collar is suffused internally with dusky pigment and has scattered blotchy black marks over much of its "pallial" surface. A longitudinal black bar on the "pallial" surface is formed above the collar's edge on the right side, at the level of the renal pore. The spongy tissues in the body wall contained many white bodies - "calciferous concretions" - which show externally as white specks scattered over the head-foot. Concentrations of these white specks occur on the edges of the snout and tentacles, and especially in a median band on the frontal region between the eyes, and at the mesial edges of the optic sinuses. The head-foot of many specimens has a heavily frosted overall appearance because of a great abundance of such granules. In some specimens the granules are very sparse. Generally, the surface of the visceral mass (especially the major liver) under the thin body wall is abundantly laced with a pattern of such concretions, which bear a relation to an arterial pattern (cf. Figs. 24 and 48).

FIGURE 6. The digestive tract, with cross sections of the same, and with the 2 livers (the "right and left lobes" of authors) and salivary glands omitted, from a preserved specimen having a shell 27 mm long. The tract has been oriented, with the "intrinsically dorsal" side (in large part not topographically dorsal) largely in view, while the sections are oriented with that side upward, and with the left side relative to that, to the left. The cecum is positioned in the "dorsal" midline in that region of the tract. The topographically dorsal side of the tract anterior to the gizzard is in view. The small dark "ventral" area in sections of the intestine represents a medial artery and a concentration of finer vessels. Stippling indicates dusky granular pigment, which generally is associated with arterial vascularization. The shown parts of the tract are rather densely ciliated throughout, except in cuticularized areas in the buccal mass and gizzard, and


salivary gland duct
dorsal food channel
buccal glands
A
C
B
D
circular muscle
gastric nv.
sinus
tendon
gizzard compressors
cuticle
tendon
gizzard tensors
mt. f.
dorsal passage
cl. s.
re. p.
mj. f.
pc. p.
vn. f.
re. p.
minor fold
do. p.
ciliated strip
major fold
pc. p.
ventral fold
E
F
G
caecum
costal grooves
l. h. d.
H
I
atrium
typhlosole
pellet compressor
raphe
circular muscle sleeve
sinuses
costae
rectal passage
anus
L
K
J
5 mm

6

except perhaps in other very limited areas. Fine muscle fibers, suggested by fine lines in the sections, are abundant throughout the system.

A to B - buccal mass; C to D - proesophagus; D to E - postesophagus; E to F - crop; F to G - gizzard; G to H - pylorus; H to I - prointestine; I to J - midintestine; J to K - postintestine; and K to L - rectum.

The anterior and posterior loops of the tract (cf. Figs. 2 and 48) are represented by the portions extending from G to I and from I to J, respectively. The rectal passage is a major venous passageway which encloses the rectum and part of the postintestine; it lies behind the lung. Note the evidence of gastropod torsion in the twist in the esophagus, near the crop: a pair of gastric nerves in the esophageal wall shows a corresponding twist. The larger folds shown in the sections generally would appear smoother in life, and somewhat different in contour, in different specimens which are preserved. The circular muscle sleeve of the rectum is covered by a vaguely papillate tissue, which is apparently glandular. In life, the buccal mass and gizzard are bright red, presumably because of the presence of muscle hemoglobin.

FIGURE 7. Median member of the tripartite jaw apparatus (cf. Fig. 15) of 2 specimens, showing the anteroventral face. A median cusp occurs in some snails. Slight asymmetry seems to be an intrinsic feature of this anterodorsal jaw. Also, the free margin may be unevenly modified by wear, or by breakage, resulting from feeding activity in which a rather coarse sand, which forms the substratum of the habitat, is ingested in quantity. The 3 jaw elements are elaborations of a cuticularized membrane which covers the adjacent buccal epithelium, and as such are continuous with each other to some extent. They have a fibrous internal structure, with the fibers arranged more or less vertical to their free edge.

FIGURE 8. The radula, 3 mm long, of a specimen having a shell 22 mm long, shown flattened out, with teeth (cf. Figs. 12, 15 and 17), of the median row and 4 transverse rows indicated by dotted lines. It bears about 11,648 teeth, the maximum number found in the population, arranged in about 91 longitudinal and 116 transverse rows (gross formula: 45-1-45). The largest radula, from a specimen having a shell-length of 28 mm, was 3.1 mm long, but it bore somewhat less than 10,000 teeth. The transverse rows may be nearly straight, or not, depending on how one straightens out the radula, but the indicated W-pattern apparently is intrinsic. The teeth and their supporting membrane are assumed to be chitinous. At or shortly after hatching of the snails, the radula is almost as wide as it is long, and it measures about 0.3 mm x 0.4 mm; then it has somewhat more than 40 transverse rows, and it shows a gross tooth formula of about 7-1-7 (15 teeth per transverse row). The number of transverse rows is about 100 in specimens about 5 mm long; in snails about 22 mm long the number averages about 112, but varies from about 94 to 128. With growth, the radula increases markedly in length, relative to its width. When the snail reaches shell-lengths of roughly 5 mm, 12 mm and 18 mm, the number of teeth in half a transverse row is about 24, 31 and 40, respectively. For snails above that size, the average was about 43. In specimens having a shell-length only of about 2 mm, 2 or 3 clearly bicuspid lateral teeth appear in each half transverse row adjacent to the central tooth: the number of those teeth doubles by the time the shell becomes 8 mm long, and in adults the number ranges from about 10 to 13. The largest radula, mentioned above, showed only 11 bicuspid lateral teeth in each half transverse row. In hatchling snails, 3 or 4 lateral teeth are differentiated from the "intermediates" in half a transverse row; then, the laterals are relatively quite

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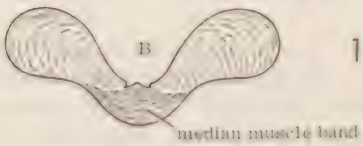

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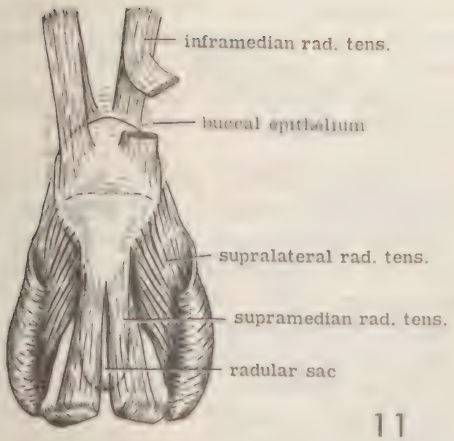

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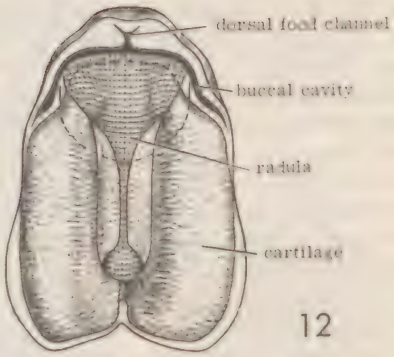

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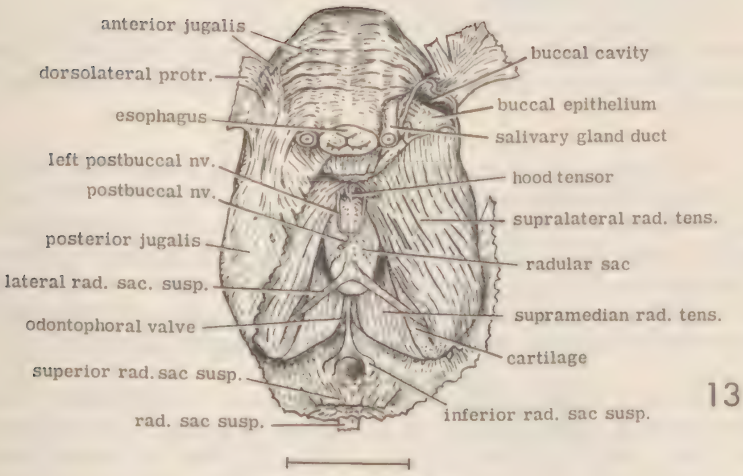

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elongate, and perhaps are weakly tricuspid.

It is impossible to make a definitive, exact radular formula for such a snail population, or a single snail. Incipient or vaguely formed teeth occur at the sides and the nascent end of the radula. Tooth counts vary from individual to individual of a given size. The count of one half of a transverse row rarely (if ever) seems to be exactly the same as that of the opposite half, and it varies somewhat along the length of the radula. It was not confirmed, but it is suspected that the number of teeth in the right half tends to be less. Up to 10, but frequently 9, cusps occurred on the marginal teeth of adults.

FIGURE 9. The buccal "cartilage," which serves as the skeletal support of the buccal mass, in right side view. A and B indicate levels of cross-sections shown in the following figure.

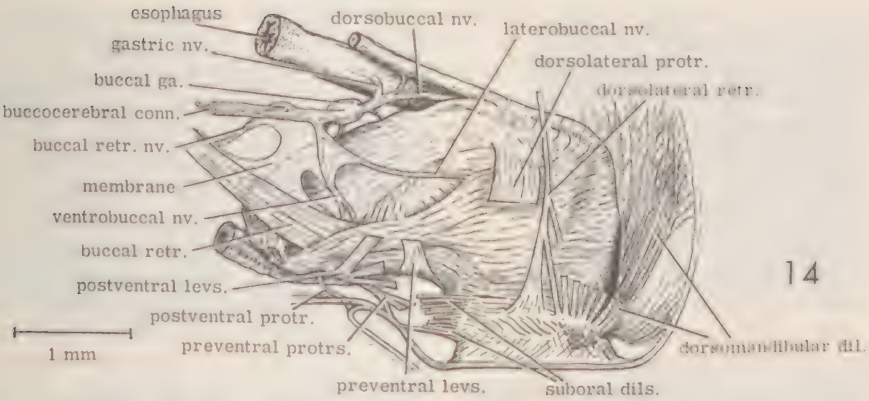
FIGURE 10. Cross-sections of the buccal cartilage made at levels indicated in Fig. 9. Stippling indicates dusky pigmentation. The tensors are numerous musculoid fibrous elements scattered within cartilage-like tissue. Near the posterior end of the organ the median muscle band is an especially discrete structure, but it becomes rather diffuse and ill-defined near the crest.

FIGURE 11. Muscles of the buccal mass which arise from the buccal cartilage and which are directly operative in movements of the radula. The cartilage has been removed from the position it would occupy in this view. The posterior end of the radula is shown in ventral view as it is rolled up cylindrically in a radular "sac" in its natural position. The other end of the radula is shown extended forward from the level of the transverse dashed line, at which it is normally bent ventroposteriad over the crest of the radula (cf. Fig. 12). The supralateral and supramedian tensors are shown in ventral view in the normal position wherein they partly embrace the cartilage. The inframedian tensors have been extended forward, so as to show their dorsal faces. The surfaces of the radula facing the viewer are coated by the subradular epithelium, which encloses the radular sac and which is continuous with the buccal epithelium, at the boundary of the portion radula shown extended forward in the figure. The various tensors, then, insert on an epithelium, rather than directly on the radular membrane.

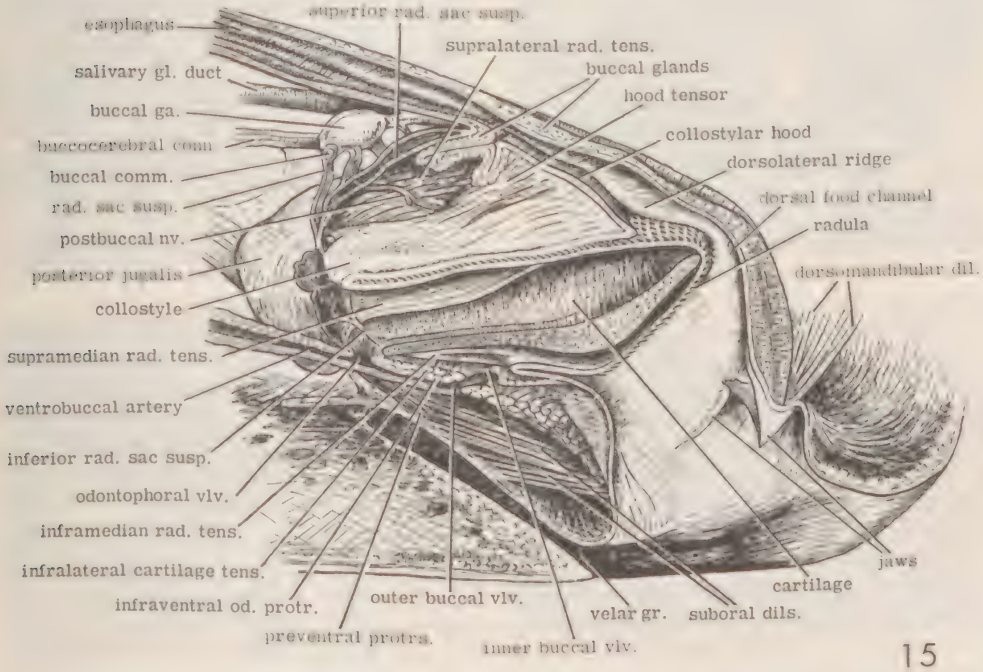
FIGURE 12. The natural positional relationship between the radula, cartilage and buccal mass, in dorsal view, with obscuring tissues removed. The resting posture of the buccal mass is indicated, exactly as in Fig. 13. Stippling indicates dusky pigmentation.

FIGURE 13. The buccal mass in dorsal view, partly dissected, with its outer tissues left in place anteriorly and on the left (cf. Figs. 14-16). The organ consists largely of muscles, of which the supralateral radular tensors (cf. Fig. 11) are conspicuously massive. The jugalis muscles form mainly a thin musculomembranous sheet which incompletely invests the buccal mass; this sheet exhibits many fine splits and perforations which are assumed to allow blood in internal sinuses of the mass to pass into the cephalopedal hemocoel.

FIGURE 14. The buccal mass, in the resting position, in right side view, showing its surface features and most of its extrinsic muscles. All of the extrinsic muscles of the right side are shown, but nearly all have been severed short of their origins on the body wall. The dorsolateral protractors (1 pair) originate


esophagus
gastric nv.
buccal ga.
buccocerebral conn.
buccal retr. nv.
membrane
ventrobuccal nv.
buccal retr.
postventral levs.
postventral protr.
preventral protrs.
preventral levs.
dorsobuccal nv.
laterobuccal nv.
dorsolateral protr.
dorsolateral retr.
suboral dils.
dorsomandibular dil.
1 mm

14


esophagus
salivary gl. duct
buccal ga.
buccocerebral conn.
buccal comm.
rad. sac susp.
postbuccal nv.
posterior jugalis
collostyle
supramedian rad. tens.
ventrobuccal artery
inferior rad. sac susp.
odontophoral vlv.
inframedian rad. tens.
infralateral cartilage tens.
infraventral od. protr.
preventral protrs.
outer buccal vlv.
inner buccal vlv.
velar gr.
suboral dils.
cartilage
jaws
dorsomandibular dil.
radula
dorsal food channel
dorsolateral ridge
collostylar hood
hood tensor
buccal glands
supralateral rad. tens.
superior rad. sac susp.

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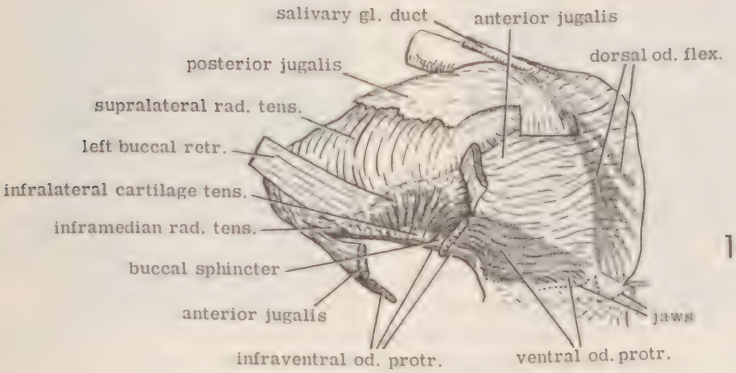

salivary gl. duct
posterior jugalis
supralateral rad. tens.
left buccal retr.
infralateral cartilage tens.
inframedian rad. tens.
buccal sphincter
anterior jugalis
infraventral od. protr.
anterior jugalis
dorsal od. flex.
jaws
ventral od. protr.

16

on the body wall alongside the mouth, and the dorsolateral retractors (1 pair), originate on the dorsal body wall. A portion of the buccal cartilage (stippled) is visible. The large ventrobuccal artery (not labelled; cf. Fig. 15) is shown entering the posterior underside of the buccal mass. The origin of the right member of a pair of gastric nerves, which innervate much of the digestive tract, is shown; these nerves run posteriorly, embedded in the wall of the tract, to the pyloric region, and they twist around the tract where the torsional twist occurs in the esophagus (cf. Fig. 6).

FIGURE 15. The buccal mass, and attendant structures, with the mass cut open just to the right of its sagittal plane to reveal the internal organization of its parts. The cartilage lies in a blood pool, bounded in part by the subradular epithelium on which the radular membrane is formed. The composite, broad projection protruding into the buccal lumen, formed by the arterior portions of the cartilage and of the hood, along with the anterior bulge of the radula, is considered to be the "odontophore." The tissue of the thick anterior wall of the buccal mass grossly resembles that of the buccal cartilage.

FIGURE 16. The buccal mass, in side view, partly dissected to show the disposition of intrinsic muscles. Two deep muscle tracts, in a grey tone, are indicated as showing through more superficial muscles; they lie against the buccal epithelium.

FIGURE 17. Unretouched photomicrographs of teeth of the radula of a large adult specimen (cf. Figs. 8, 12 and 15). The rows shown occurred in the anterior end of the radular sac, where in life the collostylar hood covered them.

A. View of several "lateral" teeth of several transverse rows on either side of a portion of the longitudinal row (c) of "central" teeth. The left side in the figures corresponds to the true left side of the radula. In mounting, some of the teeth have been somewhat displaced out of alignment. The numbers 1, 2 and 3 designate the first, second and third lateral teeth according to established practice. The focus is generally on the cusped reflections of the teeth, so that the bases of the teeth are well out of focus and barely visible; however, the outline of the angular juncture of the base and the reflection show through the latter. The reflection of the central teeth is somewhat asymmetrical, with one main cusp and a small one high on the right side, which is not clear in the photograph. Note that the laterals are strongly, unequivocally bicuspid.

B. View of the same teeth as in A, but with the basal attachments of the teeth showing more clearly through the reflections because of a difference in lighting.

C. Lateral teeth to the left of the central row, showing that the bicuspid condition occurs in extended, transverse series. This condition is constant along the length of the radula.

D. A greater enlargement of the first left and right lateral teeth. The same individual teeth are visible in the lower part of the field in A and B. The right tooth is out of alignment.

E. "Intermediate" teeth. In each transverse row there are few such teeth and the first is next to the last bicuspid tooth, which is largely visible at the right margin of the picture. Two intermediate teeth are in full view, and a portion of one to the left is visible. These intermediate teeth are essentially tricuspid, but note that supernumerary cusplets occur.

F. Teeth adjacent to the last tricuspid intermediate tooth to the left in the transverse series. Two tricuspid intermediate teeth are largely visible to the right.

A

B

C

D

F

E

G

H

one above the other. The tooth nearest the center of the field may be termed either an intermediate or a "marginal" tooth. The teeth to the left of it are marginals, which are multicuspid.
G. "Marginal" teeth, from a position to the left of the teeth in the preceding view. They are the most numerous type on the radula, many occurring per transverse row.
H. Marginal teeth from near the left border of the radula. Still further to the left, these give way by a rapid transition in form to a few much smaller, faint, incipient or vestigial teeth having a rodlike or rectangular outline and no cusps. The latter are the "most marginal" dental elements in the transverse series.

FIGURE 18. The pyloric region of the digestive tract, cut along the "ventral" side (cf. Fig. 6) and opened to show surfaces facing the lumen. Those surfaces are ciliated overall. A preserved specimen is figured: the larger folds are smoother in life.

FIGURE 19. A portion of the prointestine, opened "ventrally," showing its inner surfaces. The cut edge on the left would directly join the cut edge shown in Fig. 18. The typhlosole and raphe lie along the black arterial line shown in Figs. 2 and 48. The longitudinal riblets between the costae are markedly ciliated, well defined entities. The pseudoraphe is a vague elevation running along the intestine on the wall opposite the raphe. The pattern of costae and related elements shown extends to the rectum.

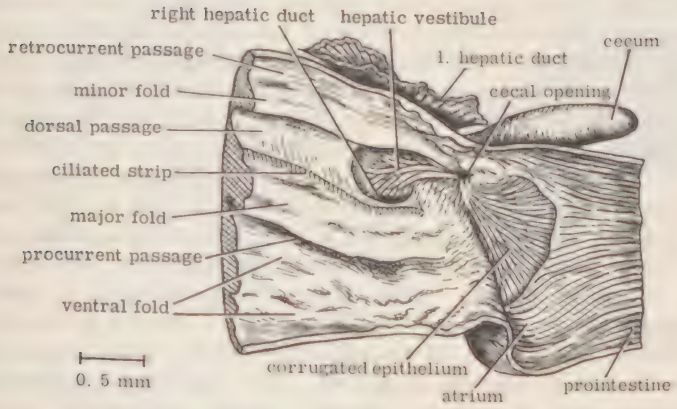
FIGURE 20. Cross-sections of the pyloric cecum, A near its base, and B, near its tip. The cecal "string," which presumably consists of waste matter derived from the liver, lies in an excurrent "tubule" which communicates with the other "tubule" along its length. In living dissections, the "strings" may be seen as spindle-shaped objects being rotated and propelled outward by ciliary action, within the indicated cavity.

FIGURE 21. Cross section of structures at the angle of the body whorl, showing the postintestine lying in a venous sinus, the rectal passage, its passageway lying behind the lung. The section is near the mid-length of the passage. The connectives are fine, spaced strands traversing the sinus in a ladder-like arrangement; they evidently act as suspensors and "flatteners" of the gut. In life the passage is filled with blood, derived from the visceral hemocoel. Finer fibers shown in it are apparently arterial in part.

FIGURE 22. Section comparable to that in the preceding figure, but made at the terminal region of the rectal passage, in which the rectum is suspended. The connectives evidently partly act as dilators of the rectum. The muscle sleeve is coated outwardly by a somewhat pustular fleshy tissue, which looks as if it were glandular. Many fine diagonal muscle fibers are arranged in the rectal folds so as to function in depressing or retracting them.

FIGURE 23. The gizzard and adjacent alimentary structures of a specimen of hatching size, indicating by comparison with Fig. 6, ontogenetic modifications in proportions of the parts.

FIGURE 24. The major, posterior, or "left" liver (the posterior liver "lobe" of authors), showing its normal contours and relationships to attendant structures.



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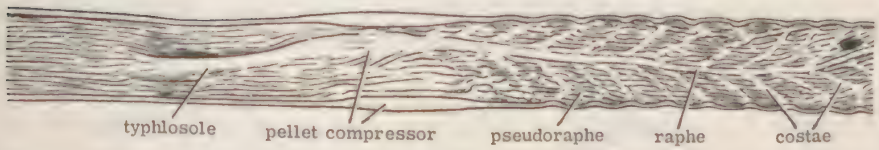

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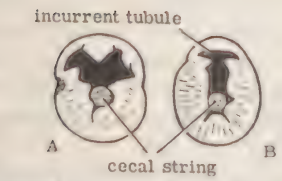

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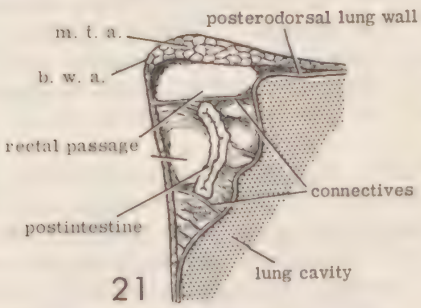

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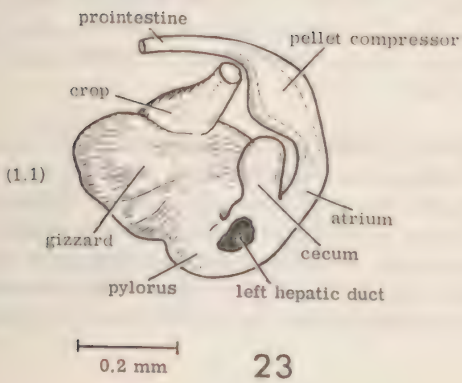

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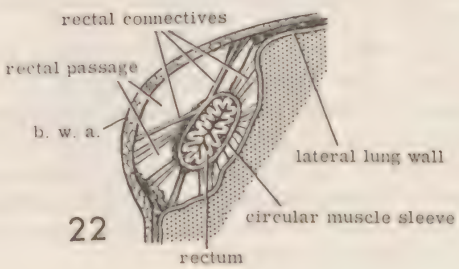

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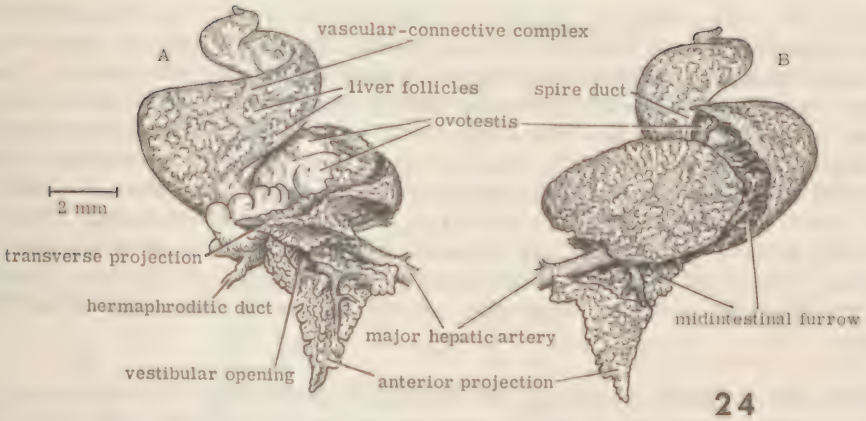
as found in the natural position in the shell. In A, the more nearly ventral aspect is in view, and in B, the exactly opposite aspect is shown. The anterior projection lies along the upper inner lip of the shell in its normal position. The mid-intestine occupies the indicated furrow in life, from which it has been removed after severance of its many arterial connections (partly shown) with the indicated vascular-connective tissue complex. Stippling indicates dusky granular pigment. The figured specimen shows greater development of the pigmented mass of tissues, relative to liver tissue, than is typical. This condition apparently resulted from a slight trematode infection. Very numerous fine musculoid fibers occur throughout the vascular-connective complex and on the outer wall of the liver, which to some extent is coated by a fine musculomembranous tissue. The liver shows strong pulsating action in life, and different portions of it contract independently of other parts. The liver tissue as such is very soft and of a practically semifluid consistency. Its living color seems to be affected considerably by dietary factors; it is usually tan, but it varies to shades of orange, yellow or brown, and it may be greenish. The vascular-connective complex is made up in large part of arterial vessels which bear white "calciferous concretions" in tissue which sheaths them. These coarsely granular concretions may be sparse or very abundant, according to the individual. Commonly they form a conspicuous white reticulate pattern over the surface of the mass formed by the liver and its attendant tissues.

FIGURE 25. The entire major liver: A, untwisted and flattened out, freed of non-hepatic obscuring tissue and viewed on its columellar face; and B, its large anterior division, separated and viewed on the opposite face. The main branches of the liver's lumen are indicated in a grey tone. Note the unilateral seriate branching of the spire duct, which passes along the columella of the shell to the apex of the animal. The vestibular opening of this liver is equivalent to the indicated outlet of the left hepatic duct, at the hepatic vestibule, in Figs. 6, 18 and 23. The spire duct consists of tissue which seems quite like that of the remainder of the organ, which is of a very soft and semi-fluid consistency.

FIGURE 26. The minor, anterior liver ("right lobe"), showing the outer, ventral face, with the relationship to certain arteries indicated. In life, the arteries fit more snugly about the organ than is shown. In some specimens this liver may be larger than indicated here and may have a much broader end (to the left) than is shown. It is a mass of irregular branches and sublobes, the whole being comparable to one of the lateral lobes of the major liver. It has a single capacious outlet, the vestibular opening into the hepatic vestibule, at the end of a very stout and short "right" hepatic duct (cf. Figs. 6, 18 and 48), which is hardly different from that of the major liver in dimensions.

FIGURE 27. Terminal liver branchlets, stained with methylene blue after preservation. The abaxial, more flattened surfaces are shown in A, and the opposite, adaxial surfaces are shown in B. Such branchlets with such ill-defined "follicles," make up the greater mass of both livers; they have large lumina which communicate widely by irregularly arranged branches with the primary branches of the hepatic lumen. Stippling indicates a pattern of histological differentiation revealed by the uptake of the stain. The internal walls of such branches are presumably ciliated to some extent.



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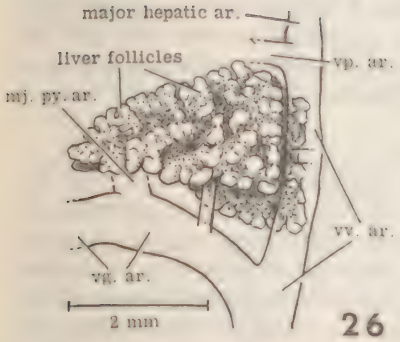

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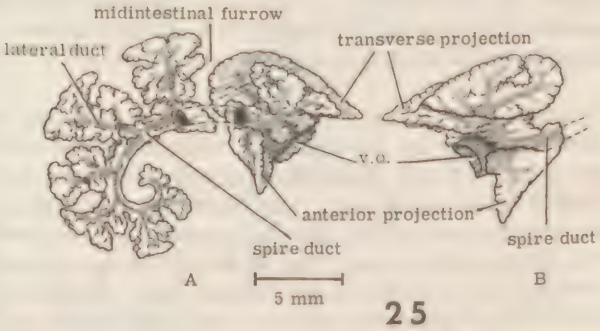

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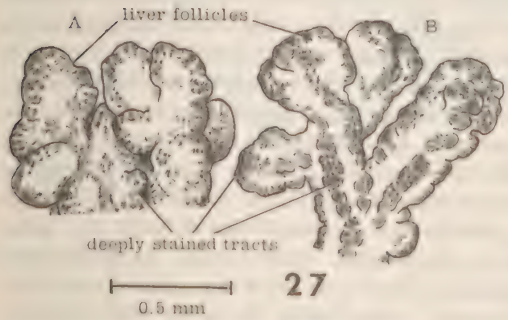

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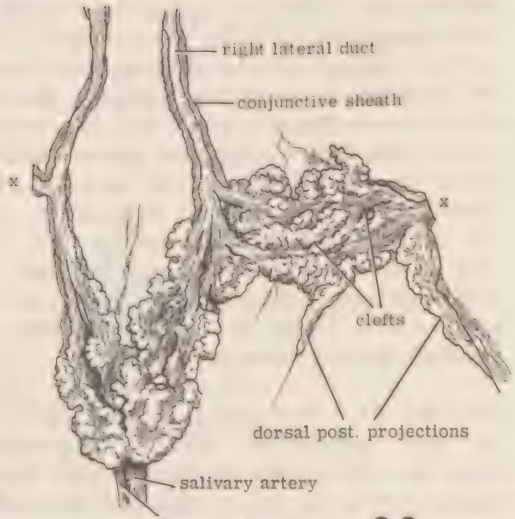

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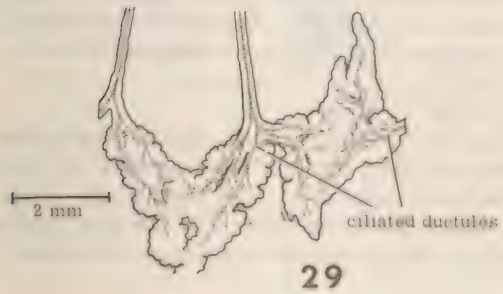


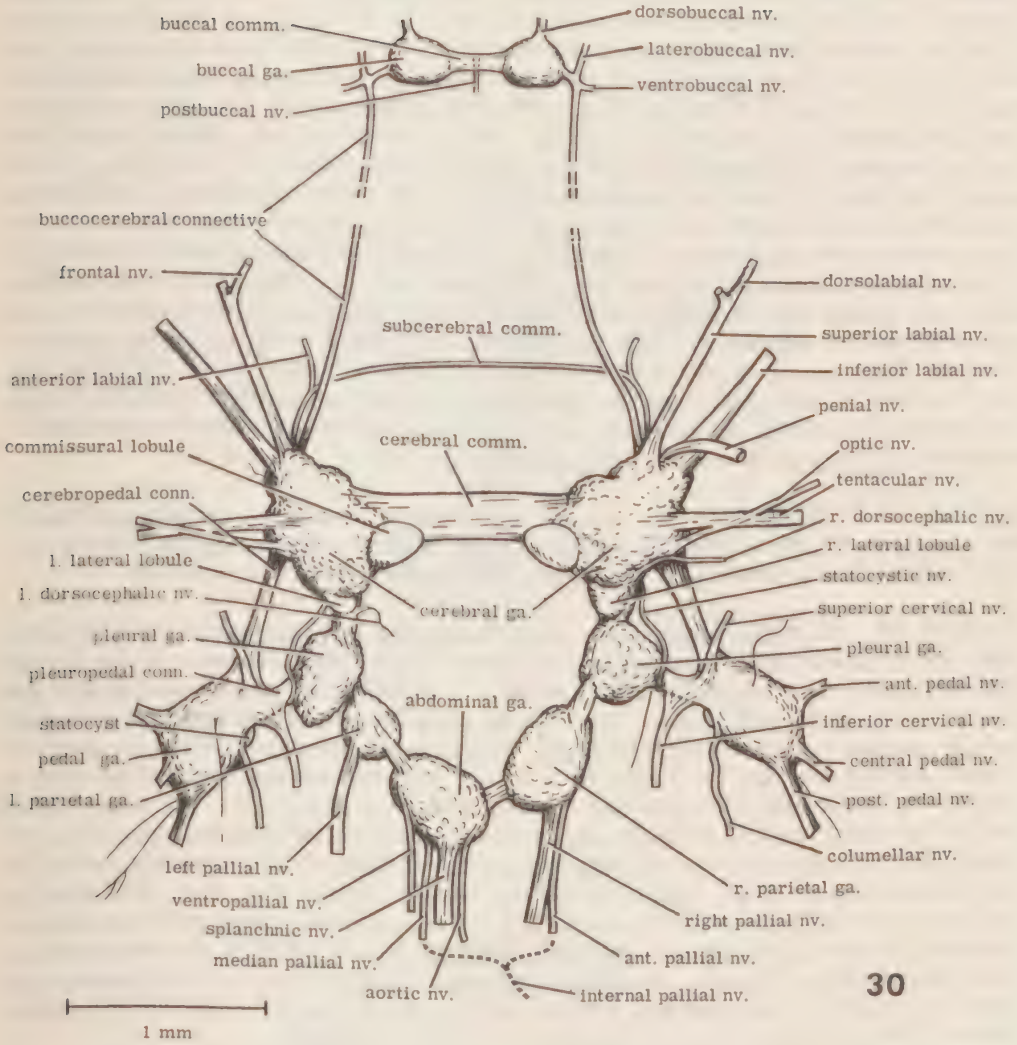
29

FIGURE 28. The salivary glands, consisting of a pair of irregularly branched organs which are held together by musculomembranous tissues. Above and below the esophagus, the glands interlock to form 2 bridging structures. The dorsal bridge has been severed from its single ductal connection on the left (x) and thrown to the right, so that the surfaces of both bridges which normally face the esophagus are in view. Note that the right and left lateral salivary ducts each give rise to a dorsal and ventral gland division, and that the dorsal division of the right duct is derived from 2 ductal branches in this specimen. The salivary retractor arises from the thinly musculomembranus surface of the sheath of the cephalic artery (cf. Fig. 32), which lies just ventral to the salivary glands. The salivary artery connects with the cephalic artery near where that retractor arises.

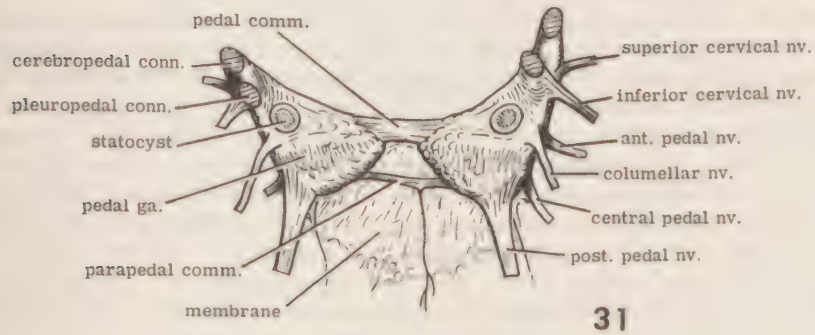
FIGURE 29. Salivary glands of a second specimen, arranged as in Fig. 28, and drawn to a smaller scale. It represents one of the many individual variants in form that occur, and shows partial fusion of the 2 ductal outlets of the right dorsal division and the presence of ductules in the glands. The ductules and the lumen of the lateral ducts are narrow and have prominent ciliation which is visible through the tissues as a golden sheen. The ductules apparently branch repeatedly to lead into numerous follicles.

FIGURE 30. The central nervous system or ganglionic collar (cf. Fig. 2), shown largely in dorsal view, with adjacent parts of the nerves arising from it. Seven ganglia and their connectives, including the cerebral and abdominal ganglia, form a ganglionic loop, the visceral (posterior) "nerve" loop, which encircles the esophagus in the natural position. The pedal ganglia and their connectives and commissures, together with the cerebral ganglia, also encircle the esophagus, forming a pedal (anterior) nerve loop; in the figure, however, the pedal ganglia have been separated from their subesophageal interconnecting commissures (pedal and parapedal; cf. Fig. 31) and are spread laterally so that their lateral faces are in view. The subcerebral commissure passes under the esophagus. The median and anterior pallial nerves join beyond the ends shown, as indicated by the dashed line (cf. Figs. 32 and 35). The buccal ganglia lie on the buccal mass. A tough membrane (not shown), continuous with a conjunctive sheath which coats the ganglia, is stretched between the several nerves of each cerebral ganglion and between those nerves and the cerebropedal connective of each side. Such tissue also floors the space shown encircled by the visceral nerve loop and subcerebral commissure. A weak, darkly pigmented, perforated, membranous sheet, the capitocerebral membrane, passes from one superior labial nerve to the other transversely, and to the anterior body wall, so as to roof a space enclosing the buccal mass. In life the ganglia are brilliant red and orange, with localized tones of blue-green and other colors. The structures labelled as lobules are bright yellow to somewhat orange, and they are assumed to have a neurosecretory function.

FIGURE 31. The pedal ganglia, in dorsal view, separated from the remainder of the ganglionic collar, and shown as they are joined together in life, with the statocysts shown in their superficial position. The dots in the latter represent the presence of many brilliant white granules, which in life are easily seen to be in a continual state of agitation, which causes a shimmering effect.


buccal comm.
buccal ga.
postbuccal nv.
buccocerebral connective
dorsobuccal nv.
laterobuccal nv.
ventrobuccal nv.
frontal nv.
subcerebral comm.
anterior labial nv.
commissural lobule
cerebral comm.
cerebropedal conn.
l. lateral lobule
l. dorsocephalic nv.
cerebral ga.
pleural ga.
pleuropedal conn.
abdominal ga.
statocyst
pedal ga.
l. parietal ga.
left pallial nv.
ventropallial nv.
splanchnic nv.
median pallial nv.
aortic nv.
dorsolabial nv.
superior labial nv.
inferior labial nv.
penial nv.
optic nv.
tentacular nv.
r. dorsocephalic nv.
r. lateral lobule
statocystic nv.
superior cervical nv.
pleural ga.
ant. pedal nv.
inferior cervical nv.
central pedal nv.
post. pedal nv.
columellar nv.
r. parietal ga.
right pallial nv.
ant. pallial nv.
internal pallial nv.
1 mm

30


pedal comm.
cerebropedal conn.
pleuropedal conn.
statocyst
pedal ga.
parapedal comm.
membrane
superior cervical nv.
inferior cervical nv.
ant. pedal nv.
columellar nv.
central pedal nv.
post. pedal nv.

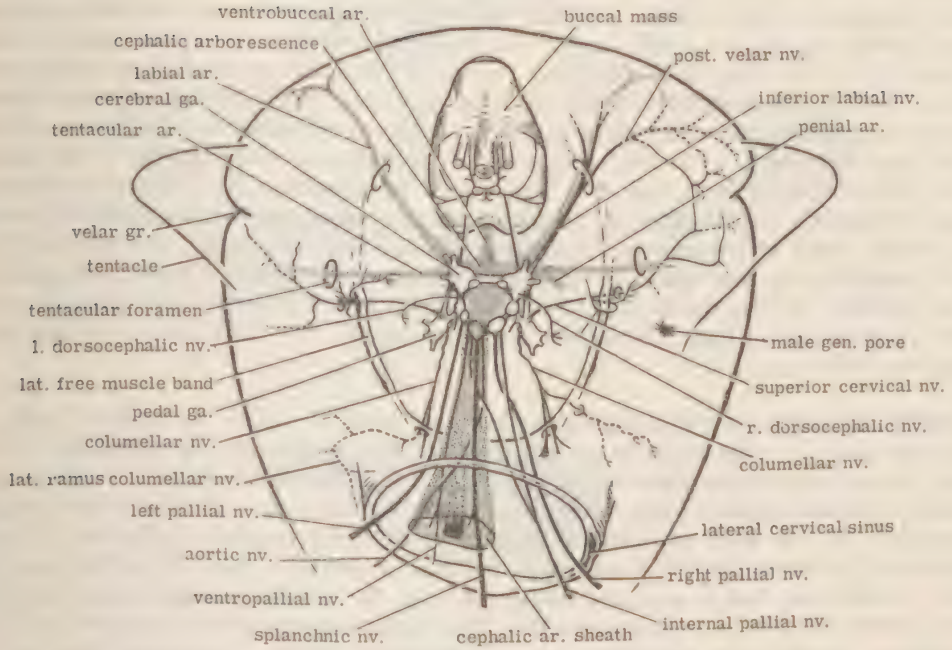
31

FIGURE 32. The central nervous system, partially spread apart as in Fig. 30, in position within an outline of the animal as seen in dorsal view, showing selected principal nerves and associated vascular structures. The cephalic artery, with the esophagus lying over it, passes through the visceral and pedal ganglionic nerve loops. It has a thick sheath of vesicular cells. Below the cerebral ganglia the artery fans out and branches to form a major arborescence, which is enclosed by and bound to the ganglia by a tough membranous tissue (cf. Fig. 30). Tissue which sheaths arteries is indicated in a grey tone. The small pair of ganglia on the buccal mass are the buccal ganglia. Portions of nerves which angle more or less ventrad are represented by broken lines; portions passing more horizontally or toward the viewer are drawn as solid lines. Nerves which have been omitted here are shown in the figures that follow. Continuations of nerves, which here are indicated as passing through the severed end of the neck, are represented in Fig. 35. The important pair of gastric nerves are seen penetrating the esophagus (cf. Figs. 6, 14 and 15). Note the anastomosis between the right posterior velar and superior cervical nerves, and the lesser associated one. Oval rings indicate foramina in the wall of the cephalopedal hemocoel.

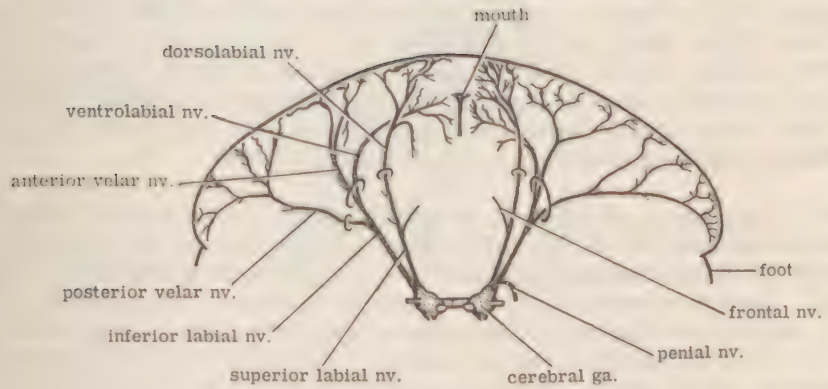
FIGURE 33. Innervation of the snout ("velum") and labial region. Note the anastomosis between branches of the left superior labial nerve. Ganglionic swellings near the mouth are indicated. A dorsal view is represented.

FIGURE 34. Principal innervation of the tentacles and dorsum of the head-foot, with the eyes and their innervation indicated. The living contours of the frontal and optic regions of the head-foot are shown. The tentacles are shown blunter and shorter than is normal in life; the nerves were traced in a preserved specimen having partially contracted tentacles. The central nervous system (in grey) is shown spread out as in Figs. 30 and 32. The dorsad and ventrad courses of nerves is indicated by solid and broken lines as in Fig. 32. The short tufted nerve branches, which attach to the ventral posterior base of the tentacles, are ganglionic in appearance, and they innervate an undoubtedly sensory epithelial area, the sensory field, which is visible externally (cf. Fig. 49). The triangle outlined over the right side of the central nervous system represents an anastomosis of nerves in the dorsal body wall, possibly one of many in the region which were incompletely traced. Such anastomoses were difficult to demonstrate and there is evident irregularity in their arrangement. In reference to structures shown at the cut end of the neck compare Figs. 49 and 51.

FIGURE 35. Nerves which pass from the central nervous system by way of the cervical portion of the cephalopedal hemocoel into the peristomial collar and to the region of the lung (cf. Figs. 30 and 32). They are represented as entering the severed base of the neck. Note that a pair of major nerves, stemming from the right and left pallial nerves, merge to form a submarginal nerve-loop encircling the collar. Also note other, smaller anastomoses in the collar near the pneumostome. The aortic, ventropallial and splanchnic nerves are attached to, or partly embedded in, the ventral side of the sheath of the cephalic artery in this region, in their natural position; in their course, they lead to the region of the genital complex near the pericardium, but there they are obscure in dissection. Further branches of the right pallial nerve are indicated in Fig. 43. The submarginal vein (stippling indicates dark pigment) is shown also in Fig. 50. The relationship of the pneumostome to a respiratory siphon is indicated in Figs. 3 and 5.


ventrobuccal ar.
buccal mass
cephalic arborescence
post. velar nv.
labial ar.
inferior labial nv.
cerebral ga.
penial ar.
tentacular ar.
velar gr.
tentacle
tentacular foramen
male gen. pore
l. dorsocephalic nv.
superior cervical nv.
lat. free muscle band
r. dorsocephalic nv.
pedal ga.
columellar nv.
columellar nv.
lat. ramus columellar nv.
left pallial nv.
lateral cervical sinus
aortic nv.
right pallial nv.
ventropallial nv.
internal pallial nv.
splanchnic nv.
cephalic ar. sheath

32


mouth
dorsolabial nv.
ventrolabial nv.
anterior velar nv.
foot
posterior velar nv.
frontal nv.
inferior labial nv.
penial nv.
superior labial nv.
cerebral ga.

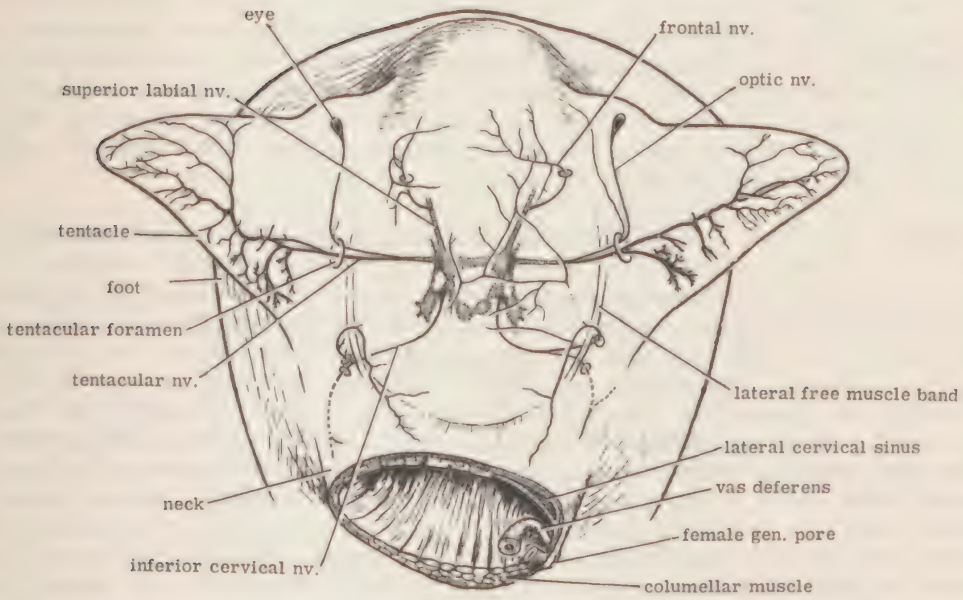
33

FIGURE 36. Nerves of the sole of the foot, in ventral view, shown within the outline of the sole of a much expanded, preserved individual. Also shown is the lower surface of the snout. In life the sole is narrower, and the edges of the lobes of the snout are much more sharp-edged and thinner. Note that the sole is biangulate at its anterolateral corners, that it is somewhat angulate in outline near its midlength, and that its posterior end is somewhat asymmetrical. Nerves coursing toward the viewer (ventrad) are represented by solid black lines: those coursing away, by broken lines; and those passing more nearly in the plane of the drawing are rendered in a grey tone. A considerable number of anastomoses of nerves are visible. It is suspected that many more anastomoses would have been found if the nerves would have been traced further. Several shorter nerve branches in the anterior part of the foot are distinctly kinky, and tend to be thickened; in life, these pass among clusters of cells protruding from the inward surface of the sole epithelium (cf. Figs. 2 and 15). The latter undoubtedly are gland cells.

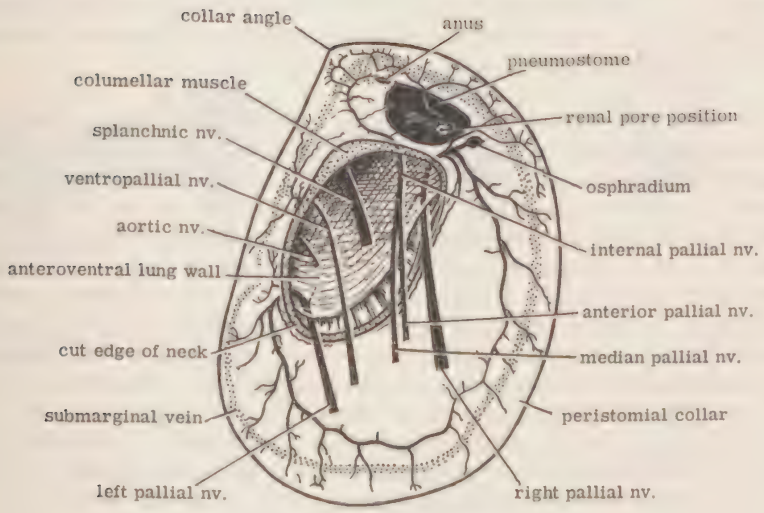
FIGURE 37. Eyes of 2 specimens, in lateral view, A and B, and another eye, in anterior view, C. The latter is the left eye, the flatter margin being mesial. The outer tissue of the pigmented cup is pink in life. The black areas in the figure are densely black in nature. The optic retractors form a loose mass of fibers which originates on the body wall at the base of the nearest tentacle. The eye is only moderately retractable. The resting position is shown in A, the retracted position in B. Each eye lies in an optic sinus (cf. Fig. 5), which communicates with the cephalopedal hemocoel rather broadly. The optic suspensor traverses that sinus vertically, attaching to its upper, lower and lateral walls. The epithelium of the outer surface of the optic bulges (cf. Fig. 34) is transparent and apparently is the "cornea" of authors. When alive, the eye tends to be contoured more as in B, and when preserved, more as in A.

FIGURE 38. The osphradium (cf. Figs. 3 and 35), showing its appearance in a preserved specimen (A), and semidiagrammatically showing its internal, ciliated, bifurcate canal (B). In life the ganglion is smoother than is shown in A. The pit lies on the wall of the mantle collar just anterior to the base of the siphon; it is difficult to see, and a small, faint, petaloid design centered on it, marks its location. The "design" seems to result from a differentiation of the epithelium, and some faint folds slightly emphasize it. The ganglionic, larger part of the organ is whitish, but the 2 protuberances are yellow in life.

FIGURE 39. The kidney of a large individual, viewed on its ventral curvature, showing its precise outline (cf. Fig. 43), its 3 divisions, its double renal muscle, and the funnel by which the pericardial cavity communicates with the renopericardial duct. Dots are used to suggest crystalloid, refractive granules (of uric acid?) which usually are abundant in the epithelium of the indicated region. That region has a golden or brilliant yellow color in life, while the other regions are paler and nearly transparent. The outline shown represents the marginal contours of the epithelium bounding the lumen of the organ, and it was determined in a bleached specimen; investing extrarenal pigmented tissues ordinarily quite obscure the organ's form. The organ, except for its spongy-fibrous division, may be viewed as a capacious long tube of renal epithelium, which repeatedly bends sharply anteriorad and posteriorad in its course. Its sinuate bends are closely crowded, and as a result the organ appears to be about 3 times as broad, and much shorter, than the tube of which it is composed. The sinuate pattern


eye
frontal nv.
optic nv.
superior labial nv.
tentacle
foot
tentacular foramen
tentacular nv.
lateral free muscle band
lateral cervical sinus
vas deferens
female gen. pore
columellar muscle
neck
inferior cervical nv.

34


collar angle
anus
pneumostome
columellar muscle
renal pore position
splanchnic nv.
osphradium
ventropallial nv.
internal pallial nv.
aortic nv.
anteroventral lung wall
anterior pallial nv.
cut edge of neck
median pallial nv.
peristomial collar
submarginal vein
left pallial nv.
right pallial nv.

35

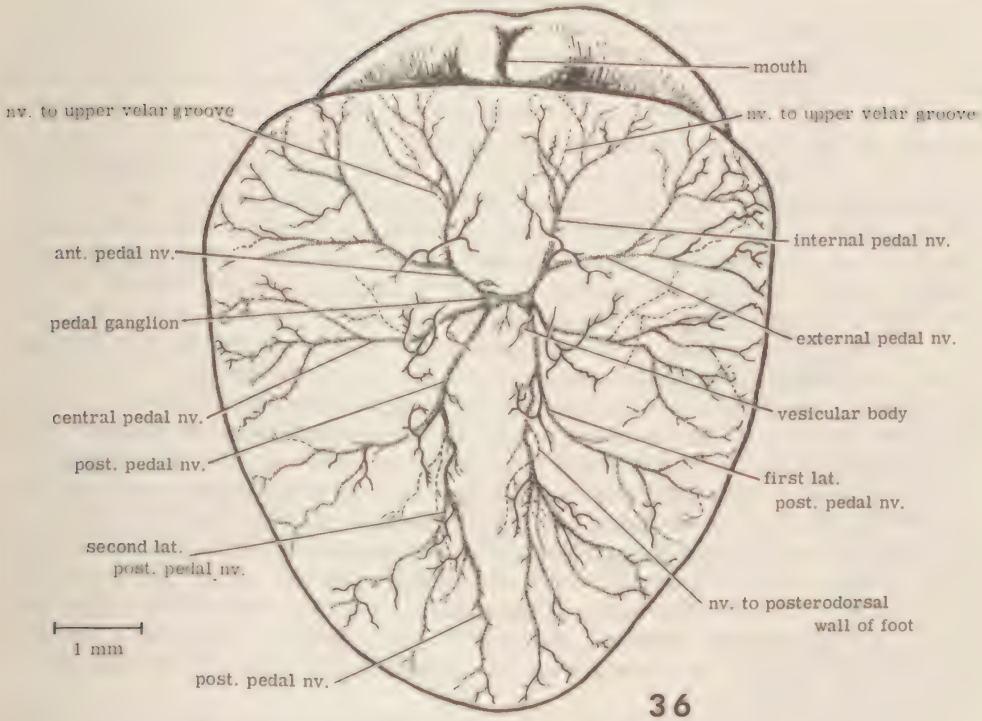
is modified by irregularities in the crowding of the bends, and by numerous lamellar invaginations of the epithelium which are largely but irregularly built on the 2 alternating series of clefts formed between the bends. Branching and anastomosing of the lamellae further obscure the pattern. The spongy-fibrous division of the organ may correspond to the nephridial gland of certain snails; it is markedly different in texture from the other divisions (cf. Fig. 42). It is very thinly drawn out at its edges, which may be very difficult to define. The dashed line (42) relates to Fig. 42.

FIGURE 40. The end of the ureter of the kidney (right dorsolateral aspect; cf. Fig. 3), with the overlying pallium and its attendant tissues removed. The outer surface of the thin renal epithelium is in view. The transverse depression forming the suprarenal channel is a highly significant feature of the circulatory system (cf. Fig. 50). A roof of partly muscular tissue is formed over this channel and over the portal vein indicated. Various muscle strands in the region evidently can elevate or depress the floor of the channel, or control the size of its inlet, which is shown on the right at the "heel" of the ureter, where an attached muscle strand is indicated. The lamellar grooves mark the lines of invagination along which internal renal lamellae are formed. Formed along the same lines are numerous cylindrical venous canals, which pass from the renal portal vein by the renal inlets, into spaces within the lamellae, in 2 series, one along the organ's more dorsal border and the other along its more ventral border. This arrangement of inlets occurs throughout the ureter and the main excretory division of the kidney.

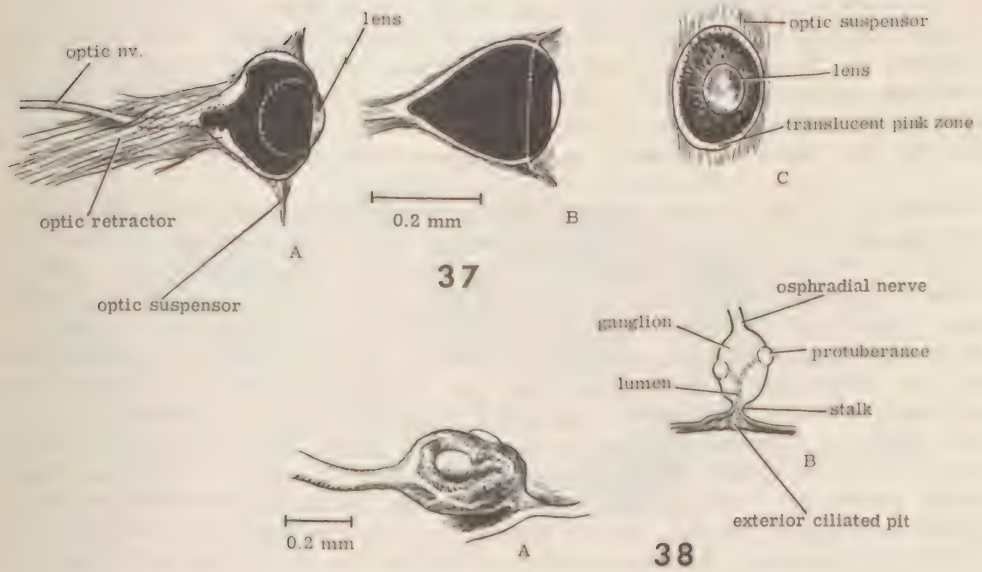
FIGURE 41. The portion of the ureter shown in the preceding figure, but with the roofing epithelial wall removed to show the floor of the renal lumen. The large longitudinal lamella possibly connects with a blood sinus enclosing the osphradium, and with sinuses associated with the function of the siphon (cf. Fig. 3). This and other lamellae of the ureter consist of a thin and membranous epithelium of an amber color.

FIGURE 42. View of the interior of the main excretory division of the kidney, and of its attendant structures, as exposed by a cut made through the left lateral wall of the lung, transverse to the kidney (cf. Figs. 2 and 4). The cut was made at the level indicated by the dashed line (42) in Fig. 39. For its entire length, the kidney (including the ureter) lies between two musculomembranous strata formed by a "splitting" of a thin general muscular stratum which lies in the lung wall between the epithelia (both pallial) in the lung cavity and on the bodywhorl surface. Numerous close-set muscle strands and bands parallel to the longitudinal axis of the animal arise from these strata and cross "over and under" the kidney transversely. In large part, these muscular elements do not completely separate from these strata, but split off, run a short distance, and then merge with them again. They particularly split off as they cross the kidney. The most prominent of these muscle strands are derived from the suprarenal muscle bands, of which some are lateral, as are those in the figure. The generally weaker strands against the ventral curvature of the kidney interlace with the renal muscle. In the figured region the renal epithelium is applied intimately to both the former and latter muscle elements. However, along much of the length of the ureter the latter are weakly developed, and a bed of spongy tissue largely separates the epithelia of the kidney and the lung cavity.

Two series of lamellar buttresses run along most of the length of the kidney,


mouth
nv. to upper velar groove
nv. to upper velar groove
internal pedal nv.
ant. pedal nv.
pedal ganglion
external pedal nv.
central pedal nv.
vesicular body
post. pedal nv.
first lat. post. pedal nv.
second lat. post. pedal nv.
nv. to posterodorsal wall of foot
1 mm
post. pedal nv.

36


lens
optic nv.
optic suspensor
lens
translucent pink zone
C
optic retractor
0.2 mm
B
A
optic suspensor
osphradial nerve
ganglion
protuberance
lumen
stalk
B
exterior ciliated pit
0.2 mm
A

37

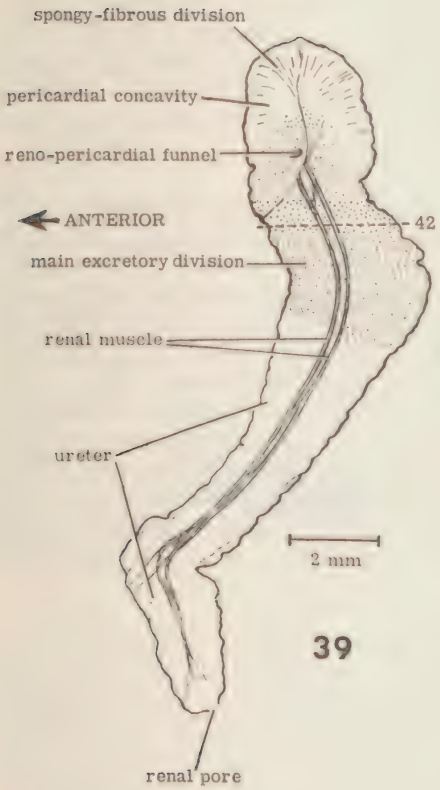
38

one against the anterior renal wall, the other against the opposite wall. They fit into the clefts formed between bends of the renal tube. There are perhaps about 30 in each series, and those of one series tend to alternate with those of the other. Those of the anterior series are more prominent. Within the series they are variably developed, some being poorly defined. In the ureter they are generally rather small and weak and in the figured region they are well-developed. Structures of somewhat similar nature occur in the spongy-fibrous renal division. The buttresses are reinforced by rather rigid musculoid thickenings of their free, concave borders, and by similar linear thickenings running in or on their surfaces in several directions. The epithelial renal lamellae, at their anterior and posterior ends, tend to be formed on the buttresses. Each buttress is sandwiched between 2 layers of renal epithelium which cling to it tightly. In the figure the epithelium has been stripped from the 2 buttresses in view, and it has been removed some distance beyond the plane of the cut. The 2 coarse dashed lines indicate the original anterior and posterior limits of the renal epithelium that has been removed. The epithelial lamellae of the main renal division have thicker, fleshier walls than do those of the ureter, and they mostly are very densely crowded and subdivided into irregular lobes and papillae.

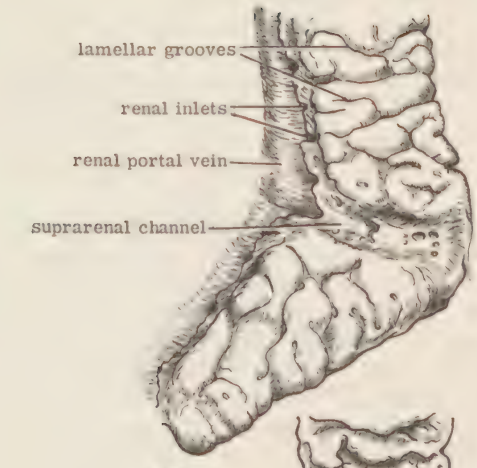
In the spongy-fibrous division the epithelium is apparently quite delicate and evaginated so as to divide the peripheral lumen radiately into a number of elongate pockets, which converge toward a reduced central lumen that is directly continuous with the primary lumen of the kidney. A distinctive, diffuse, yellowish tissue of finely spongy texture surrounds the pockets. Musculoid fibers lie within that tissue, and they are partly fused with fine membranous buttresses of the invaginations.

The vena cava is a venous canal which carries all of the body's blood to the heart. Two series of cylindrical outlets are indicated in this canal; these series are continuous with similar series in the ureter (cf. Figs. 40 and 50). The walls of the vena cava and the renal portal vein seem to be formed largely by the coalescence of musculoid strands which issue from adjacent tissues and become tangentially arranged to the lumen of those vessels. The massive bed of tissue (cf. Figs. 3, 4 and 50) shown anterior to the kidney is interlaced with numerous musculoid strands, and it chiefly consists of large globular vesicular cells having pale-blue, rather fluid, viscid contents. This tissue-bed's relationship to the vascular system may suggest that it has a lymphatic function.

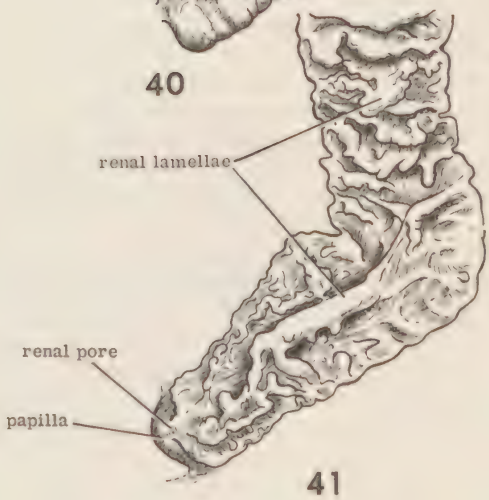
FIGURE 43. The kidney from a different adult specimen than that shown in Fig. 39, showing its topographic relationship to the pericardium (cf. Fig. 4), to certain nerves (cf. Fig. 35), and to the gland field of the lung wall. The difference in form between this kidney and that in Fig. 39 largely reflects a functional modification rather than an individualistic difference. The vena cava opens capaciously into the auricle of the heart. The origin of the cardiac nerve was not determined. The gland field (cf. Fig. 3) is a padlike elevation of the lung wall, suffused with black pigment. It is visible in an external view of the body whorl of pigmented adults as a diffusely grey patch. The pad's tissue is spongy, and embedded in it are many irregularly spaced unicellular glands. These glands are flask-shaped, with long, thin necks which extend to the epithelial surface of the pad. In life each gland cell contains many ovoid granules in vibratory motion. Pressure on the surface of the pad at the neck of any such gland causes a sudden ejection of its contents, which liquifies on release into water. Most of the glands are pale blue, but others are orange, or other colors, or brilliant white, so that the field superficially looks iridescent. During dis-


spongy-fibrous division
pericardial concavity
reno-pericardial funnel
ANTERIOR
42
main excretory division
renal muscle
ureter
2 mm
renal pore

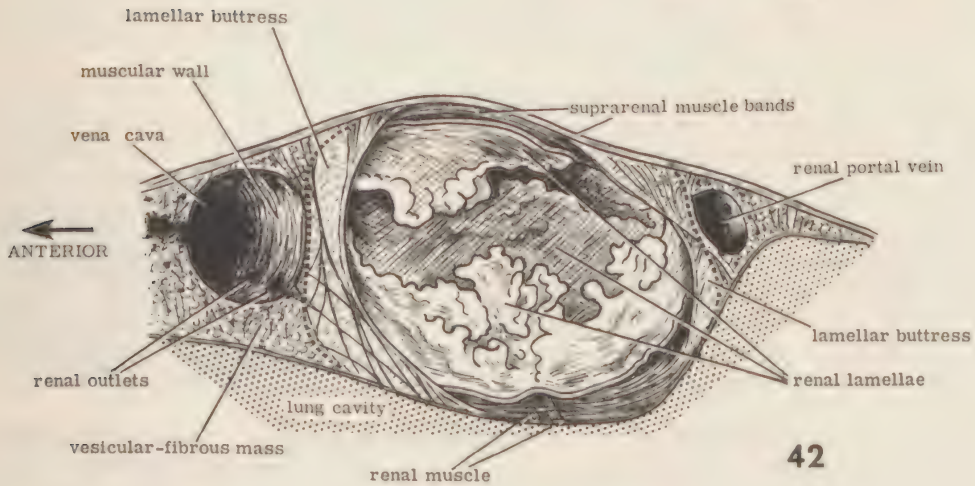
39


lamellar grooves
renal inlets
renal portal vein
suprarenal channel

40


renal lamellae
renal pore
papilla

41


lamellar buttress
muscular wall
suprarenal muscle bands
vena cava
renal portal vein
ANTERIOR
lamellar buttress
renal outlets
renal lamellae
lung cavity
vesicular-fibrous mass
renal muscle

42

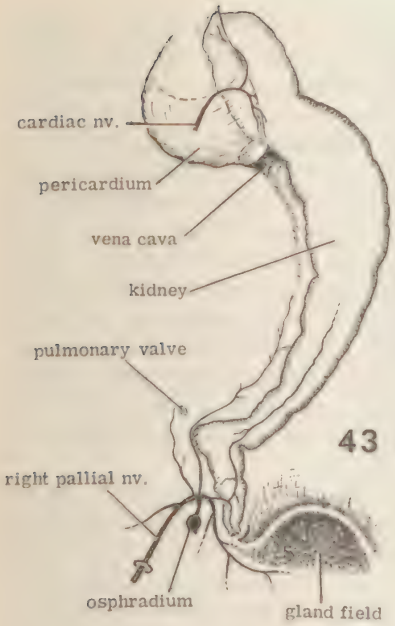
charge and dissipation, the contents retain their particular color. In very young, living, and relatively unpigmented transparent specimens, this field is quite noticeable externally even through the shell, as a granular light blue area. Similar glands are scattered on parts of the peristomial collar. This field possibly is homologous to the "hypobranchial gland" of prosobranch snails. Its slimy secretion probably is essential to the function of the siphon, and perhaps aids in removing renal waste from the lung.

FIGURE 44. The renopericardial duct and funnel (cf Fig. 39) which connect the lumen of the kidney with that of the pericardium. These passageways and attendant structures are viewed in A as if seen through the lateral, outer wall (cf. Fig. 4) of the kidney, after being stripped of the renal epithelium which coats them in nature. However, the epithelium has been left on the intra-renal lip of the duct where it opens into the kidney's lumen. The funnel is musculomembranous, and has a crescentric, tough, intrapericardial lip. The duct itself is of more fleshy tissue, and its indicated extrinsic strands of muscoloid tissue evidently serve as tensors, compressors and dilators of the duct, according to their individual position and activity in coordination with each other. A stronger, longer musculoid band involved in functional modification or bracing of the funnel is shown. In the 2 drawings the duct is flattened, and essentially closed, so that its outlet into the kidney is a broad slit. In B, the duct is shown dissected open to reveal its giant cilia.

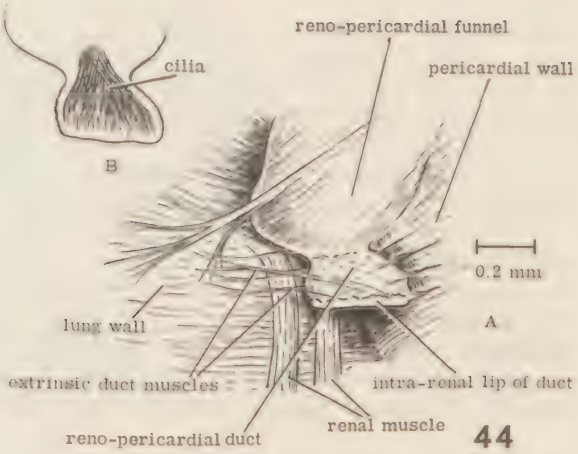
FIGURE 45. The heart of 4 preserved specimens, showing different states of contraction corresponding to functional states. In the specimen on the left a semilunar valve at the outlet of the ventricle is indicated. The longitudinal dotted line relates to Fig. 47 (A). The auricle is shown as collapsed and wrinkled, a condition which does not occur in life. The outer surfaces of the heart chambers, even when contracted, are normally smooth. The auricle can expand more widely yet than is indicated in the drawings. The vena cava probably delivers blood to the auricle with considerable force, in pulses. There is no valve at the inlet into the auricle. The ventricle is of a dense tan color. The auricle is of a similar tone, but paler, somewhat milky in appearance. White "calciferous concretions" occur in the ventricle, which is also permeated by dusky pigment.

FIGURE 46. The auricle of the heart, in outline, and a portion of its wall more greatly enlarged, as viewed by transmitted light, showing a reticulum of muscular strands which occurs over the entire inward surface facing the lumen (cf. Fig. 47). The preparation has been stained. The auricular wall is thin and membranous; the reticulum is partly fused with it, but portions of many strands pass freely through the lumen, some hanging within it as long curved loops. Nodules of 2 sizes, presumably having an excretory function, are attached to the reticulum throughout the auricle, the smaller being especially abundant. Perhaps some of the nodules are of a ganglionic nature. The inlet into the auricle is held gapingly open at all times by having the circular edge of the auricle which surrounds it attached around the circumference of the outlet of the vena cava.

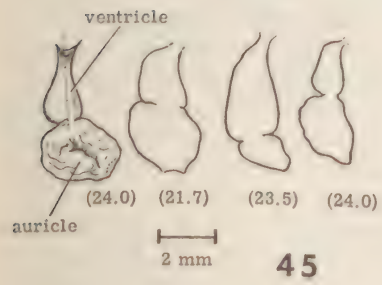
FIGURE 47. The ventricle, A, with its internal structure revealed by a longitudinal cut (made along the dotted line in Fig. 45), showing its positional relation to adjacent structures, and B, showing the semilunar aortic valve at its outlet. The ventricle as shown here is in a relatively contracted state. When expanded, the wall is much thinner and much less dense, and the muscle cords


cardiac nv.
pericardium
vena cava
kidney
pulmonary valve
right pallial nv.
osphradium
gland field

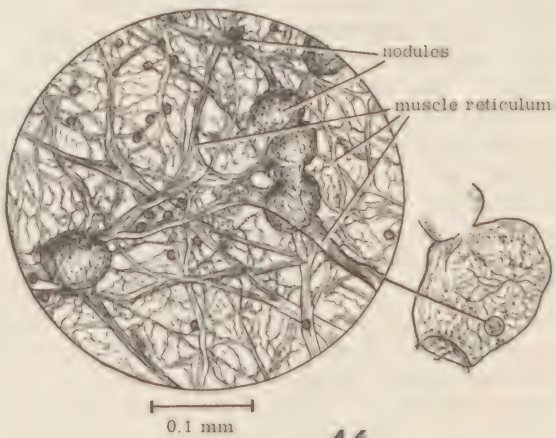
43


cilia
B
reno-pericardial funnel
pericardial wall
0.2 mm
A
lung wall
extrinsic duct muscles
intra-renal lip of duct
renal muscle
reno-pericardial duct

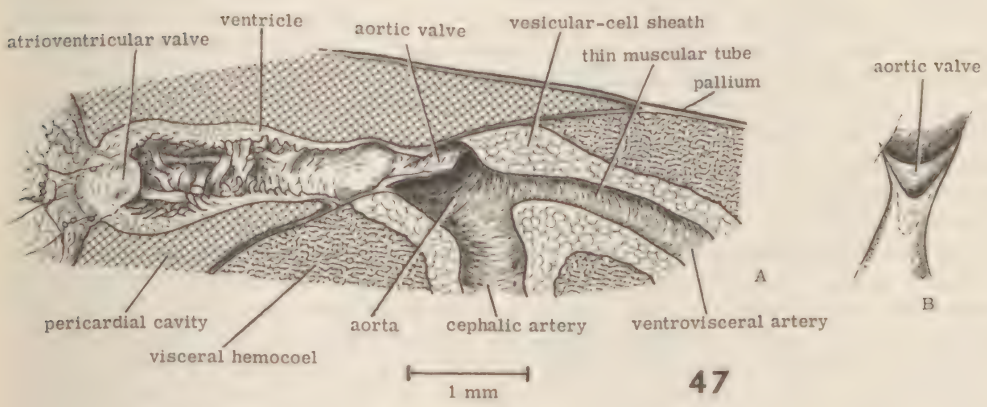
44


ventricle
auricle
(24.0)
(21.7)
(23.5)
(24.0)
2 mm

45


nodules
muscle reticulum
0.1 mm

46


atrioventricular valve
ventricle
aortic valve
vesicular-cell sheath
thin muscular tube
pallium
A
pericardial cavity
visceral hemocoel
aorta
cephalic artery
ventrovisceral artery
1 mm

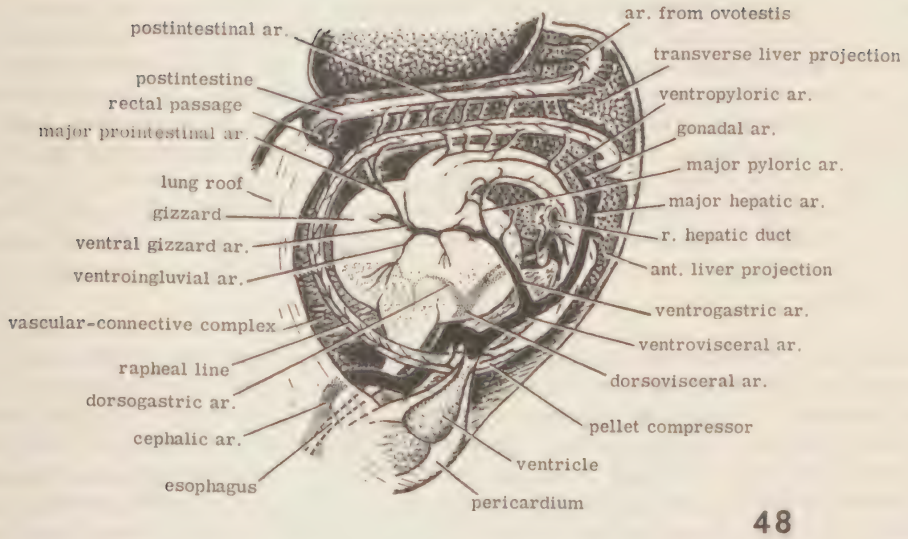
aortic valve
B

47

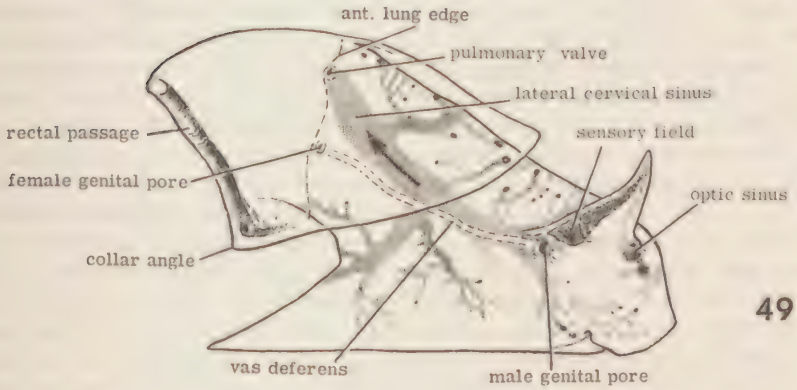
shown are much longer and thinner; the muscles then are seen to form a reticulum similar to that of the auricle (cf. Fig. 46), with strands that hang in the lumen. The semilunar valve is very thin and membranous. The atrioventricular valve consists of 2 fleshy lips, of which one has been cut away in the figure. In this preparation those lips were found directed "forward," and the valve was open. When the valve closes, its lips are vertical to the plane of the figure, and the passageway in it is a closed slit. The pericardial lumen is presumably bounded by coelomic epithelium, continuous over the surface of the heart. In B, the larger portion of the ventricular wall in view is that epithelium-coated portion exposed to the pericardial cavity, while the smaller portion enclosed by the thin broken line is an especially thin part, not so coated, which abuts on the pericardial wall. The arteries *per se* consist of the indicated thin membranous muscular tube. In adults, they generally are supported by a very thick sheath of large vesicular cells having bluish, semi-liquid contents (cf. Fig. 32). The sheath, at least in places, is coated by tough membranous and fibrous elements.

FIGURE 48. Arterial patterns (in solid black) in the visceral hemocoel, in the region of the gizzard. The gizzard and the first intestinal loop, for clarity, are shown less crowded together than is normal. Also, the edge of the lung on the lower left is shown abnormally withdrawn from the region of the ventricular outlet. The minor liver (cf. Fig. 26), which arises at the right hepatic duct (cf. Fig. 6), has been removed; in this view it would lie over the space shown between the pylorus and the gizzard, and over the nearby region of the pyloric atrium and cecum. Structures behind the gizzard (which is rendered as transparent) are shown in a grey tone; a mottled area so indicated represents a complex of partly web-like, fine vascular elements and fibrous, pigmented tissues which attaches to the albumen gland (cf. Fig. 2). Such tissues obscure the pattern of vascularization of the cecum and the nearby parts of the gizzard and liver. In life, the arteries are generally blackish, due to finely granular pigmentation. However, vesicular-cell sheaths largely hide that dark color, and generally bear abundant brilliant-white "calciferous" concretions, so that the course of major arteries are mostly marked in life by a white, coarsely granular pattern. The major exit of venous blood from this region is through the rectal passage behind the lung, into which the postintestine is shown passing on the left.

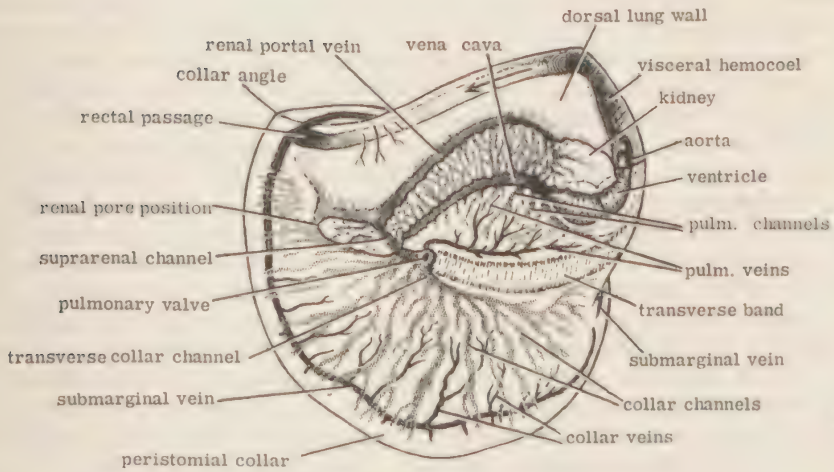
FIGURE 49. Venous pathways (grey tone) in the wall of the anterior part of the animal, as related to structures important to circulation in the peristomial collar and the roof of the lung, and as related to the living form of the cephalopedal mass in the locomotory posture (cf. Figs. 2, 5 and 50). The lateral cervical sinus (cf. Fig. 34) is capacious and it apparently drains all of the great volume of venous blood from the head-foot region (a comparable sinus is not present on the left side). Its wall is well-defined and formed of fused musculoconnective fibers tangential to its cavity. The other sinuses shown connecting to it tend to be walled similarly. The more dorsal ones are especially vein-like and lie between the integument and the muscles which roof the cephalopedal hemocoel. The blood passes from the hemocoel directly into the latter sinuses by circular perforations (indicated as black ovals) in the muscular hemocoelic roof. The muscles around those openings seem to be arranged so as to exert valvular control, and waves of contraction of fibers in the walls of these sinuses appear to propel the blood in them toward the lateral cervical sinus. An exceedingly complex network of less regularly defined sinuses drain the massive beds of spongy-fibrous tissue in the lower head-foot region; the main efferent com-


postintestinal ar.
postintestine
rectal passage
major prointestinal ar.
lung roof
gizzard
ventral gizzard ar.
ventroingluvial ar.
vascular-connective complex
rapheal line
dorsogastric ar.
cephalic ar.
esophagus
ar. from ovotestis
transverse liver projection
ventropyloric ar.
gonadal ar.
major pyloric ar.
major hepatic ar.
r. hepatic duct
ant. liver projection
ventrogastric ar.
ventrovisceral ar.
dorsovisceral ar.
pellet compressor
ventricle
pericardium

48


ant. lung edge
pulmonary valve
lateral cervical sinus
rectal passage
sensory field
female genital pore
optic sinus
collar angle
vas deferens
male genital pore

49


dorsal lung wall
renal portal vein
vena cava
collar angle
visceral hemocoel
kidney
rectal passage
aorta
ventricle
renal pore position
pulm. channels
suprarenal channel
pulm. veins
pulmonary valve
transverse band
transverse collar channel
submarginal vein
submarginal vein
collar channels
collar veins
peristomial collar

50

ponents of this network become increasingly well defined as they approach the lateral cervical sinus, where many become superficial. The blood passes from the head-foot region (as the arrow indicates) at the right anterior edge of the lung by way of the posterior termination of the cervical sinus, which is transversely blocked by the pulmonary valve. This valve is an oval, musculous membrane having a central perforation which can appear as a closed slit, or can be widely open and ovate in shape. The subtentacular sensory field relates to ganglionic tissue in the tentacle (cf. Fig. 34). The opposite tentacle shows a similar field. The vas deferens lies in the body wall where it fills a longitudinal cavity. It may be seen through the outer tissues in living specimens.

FIGURE 50. Dorsal view of patterns of venous sinuses in the peristomial collar, in the roof of the lung, and in the kidney. The circulation in these regions is here inferred from those patterns. The term vein is used for sinuses that are markedly tubular and that grossly resemble arteries in having darkly pigmented, well-defined walls. Blood from the lateral cervical sinus (cf. Fig. 49) enters the region shown through the pulmonary valve into a small space overlying that valve. That space is blocked on the left by a vertical wall of tissue forming the end of the transverse band, and behind, by a bloc of massed vesicular cells separating it from the vena cava (cf. Fig. 42). Two blood pathways lead from that space. The most capacious pathway is the suprarenal channel, which passes directly to the renal portal vein. From the latter vein the blood must pass through the network of canals in the renal lamellae (indicated in grey) to reach the heart. The second outlet from the space over the pulmonary valve always seemed to be tightly closed in preserved specimens, and it was not demonstrated clearly, but it leads into a very clearly defined, deeply pigmented branching canal, or transverse pulmonary vein, which passes behind the transverse band. That vein's branches lead deeply into the thick bloc of bluish vesicular cells lying in front of the kidney. Irregular collecting channels, having indefinite walls, arise between these pulmonary veins and pass to the vena cava. Accordingly, the blood carried by the pulmonary veins and channels bypasses the renal portal circulation. Blood from the visceral hemocoel enters this system via the peristomial collar, to which it is transported by way of the rectal passage (note the arrow). From the outlet of that passage, 2 deeply pigmented, artery-like canals (submarginal veins) arise. One passes along the columellar lip of the collar; the other passes in the opposite direction so as to encircle the remaining portion of the collar almost completely. Dark side branches (collar veins) of these pass toward the collar edge (very short ones) and toward the base of the collar. The pair of submarginal veins and their branches look much like the pulmonary veins; they terminate in beds of spongy-fibrous tissue. In these beds many extensive, irregularly defined collecting channels arise; these converge and join a transverse channel just in front of the transverse band. These channels have indefinite walls. The transverse channel leads to the small space overlying the pulmonary valve. Several gross crescentic muscular elements in the lower end of the rectal passage, and in the first part of the right submarginal vein, are positioned to act as valves preventing backflow of blood toward the visceral hemocoel. Also, a large short vein arises from the end of that passage and enters the posterior portion of the siphon (cf. Fig. 3). In life, waves of contraction can be seen sweeping along the collar border from the right side, anteriorad and to the left, indicating propulsion of blood in the right submarginal vein, and the creation of blood pressure. In special preparations, the pulmonary and collar

veins can be seen to undergo peristaltic action, and numerous fibers arranged along the channels can be seen to undergo rhythmic contractions.

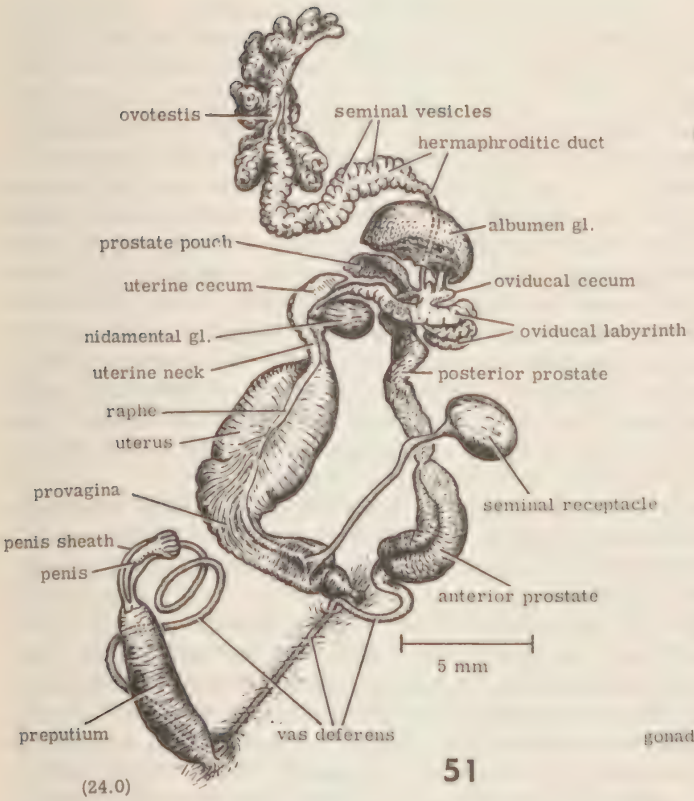
The indicated relationships suggest that the major circulatory patterns in the roof of the lung may relate more prominently to renal and hemopoietic or "lymphatic" functions than to oxygenation of the blood, and that the peristomial collar may serve the latter function to a significantly higher degree. The portion of the roof of the lung behind the kidney, and the deeper portions of the lung which are not indicated in this figure, do not show any prominent vascularization which would attest to an efficient "pulmonary" function.

FIGURE 51. The entire reproductive system of the *"angulata"* form of *Lymnaea catascopium* Say from Houghton Lake, Michigan, showing its 3 primary divisions: hermaphroditic (beginning with the ovotestis at the top of the figure), female, and male. The location of major organs of the system in the body of the snail is indicated in Fig. 2. To reveal all parts clearly, various organs are shown pulled out of their natural relative position, or straightened out as much as is necessary, and the length of the albumen gland duct and of the terminal narrow division of the hermaphroditic duct is exaggerated. The latter duct passes ventral to the albumen gland. The ovotestis is the most posterior of the reproductive organs, and it loosely fits around the columella in the spire of the snail's shell, somewhat spirally. From the apex of the gonad to the terminus of the hermaphroditic duct, the system consists of a single bisexual tract, both morphologically and functionally. However, ova develop within a zoned pattern in the ovotestis, and the hermaphroditic duct, during the adult life of the snail, functions only as a seminal reservoir from day to day, except when it simultaneously and momentarily serves as an oviduct at the onset of formation of an egg mass (cf. Fig. 57). The female and male systems arise from a common point, at the terminus of the hermaphroditic duct. Structures closely associated with this point make up what is here termed the "carrefour complex." The female tract shows 3 successive primary morphological divisions which are here thought of in a topographic sense, and partly in terms of function, as oviducal, uterine and vaginal. In a similar sense, the latter 2 divisions make up a uterovaginal division. In the natural position, the most prominent part of the uterine division, here called the uterus, has its dorsal face bulging against the floor of the lung, and its ventral face appressed to the prostatic tract. Then, the duct of the seminal receptacle is held between the latter and the female tract for much of its length. In the figure the uterus is represented as having been freed from the prostate and swung upward and over toward the right side of the animal (toward the left side of the drawing), so that it and adjacent female parts have their dorsal faces turned downward, and their ventral faces in view. The anterior prostate is shown in its natural posture with its dorsal face exposed to view. The seminal receptacle is shown near its natural relative position, in which it is adherent to the pericardium; at the indicated kink in its upper course it passes through the midbody septum which separates the visceral and cephalopedal hemocoels of the body. A large part of the vas deferens lies in the body wall of the snail. The penis, penis sheath and preputium make up the penial complex, which is capable of being everted to the outside of the animal, but which is shown fully retracted with its mesial face in view. The penis would not actually be visible in such a view but it is drawn as if it showed through the wall of its sheath. The vas passes out of the body wall into the cephalopedal hemocoel close to the preputial base; in the figure a portion of it passing lateral to the preputium is indicated in dotted outline.

The indicated size and conformity of the organs are those judged to be about average for a healthy large adult in a "resting" reproductive state. The size of the major glandular organs is rather inconstant from specimen to specimen. The drawing is based primarily on a specimen with a shell having a length corresponding to the bracketed number near the bottom of the figure (24.0 mm), but it has been modified in accordance with data on many living and preserved specimens.

Ontogenetically, the ovotestis and penial complex become identifiable, by dissection, before those of any other reproductive structures. They appear clearly in specimens that have a shell only about 4 mm long. The hermaphroditic duct becomes identifiable when the snails have grown about 2 mm longer, at which size the anterior end of the provagina, with a narrow white tube extending from it posteriorly, appears. The oviducal, uterine and prostatic tracts arise by splitting off from that tube as the snails grow from about 7 to 8 mm in length. All prominent organs shown in the figure are identifiable when the splitting becomes completed, and by then sperm (or what appears to be sperm) already begin to accumulate in abundance in the hermaphroditic duct. Abundant ova (and/or similar cells?) appear in the gonad as the snails grow from about 10 to 11 mm in length, when the penial complex takes on the adult appearance. After maturing, the reproductive system tends to grow in size as long, or almost as long, as the snail grows. While its parts tend to maintain the approximate relative proportions indicated here, growth of the major glandular organs tends to level off as the snails grow to a shell-length of about 19 mm. However, such organs may be enlarged or reduced markedly in apparently healthy individuals. A maximally robust condition of the albumen gland seems to provide the surest proof of full sexual maturity and healthiness of a snail; it tends to be the last of the organs to develop fully adult characters, in size, color and texture, and this occurs as the snail grows in length from about 13 mm to 16 mm. Unfortunately, this gland especially is subject to suppression of maturation and atrophy in relation to trematode infections, and apparently to variation dependent on nutritional factors and oviposition activity.

The hermaphrodite organs generally have a spacious lumen and thin walls; their seeming bulkiness is due in large part to their voluminous contents. The bulk of the substance of the female tract and of the prostatic structures is made up of a glandular tissue, which is supported only by a general framework of delicate tissues that are partly membranous and partly weblike, with the latter tending to form a separated outward stratum. The membranous elements seem to be formed from an incompletely fused meshwork of musculoconnective fibers, many of which interconnect with the weblike stratum. A fine network of dusky arterial vessels seems to be an intimate part of the latter stratum. The membranous tissue covers all of the organs, into most of which it is invaginated very deeply to shallowly, so as to form thin, double-walled internal supports of very numerous glandular lamellae or plicae. Extensive arterial circulation evidently takes place in the narrow spaces between the double supporting membranes. Many musculoid fibers cross over the exterior lines of invagination or pass into them, in series, and insert in the plicae and lamellae. The weblike stratum tends to form a common envelope enclosing all of the organs, which it binds firmly together wherever they lie close to each other. The membranofibrous stratum of the walls of the gland-organs merges into thick and quite muscular strata which exist in the largely nonglandular parts of the tract, as in the more anterior portions of the vaginal region. Longitudinal musculature is delicate or scarce in the reproductive system except in heavily muscular



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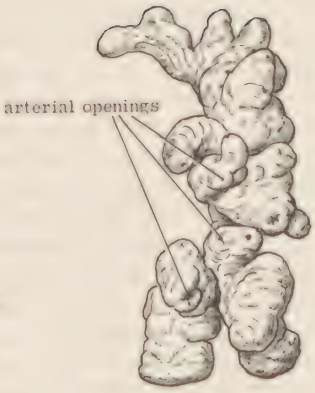

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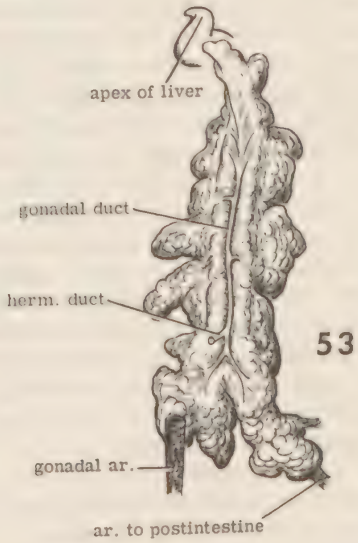

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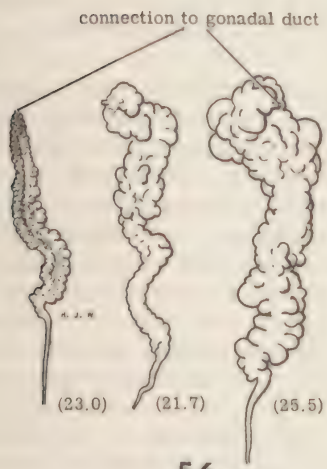

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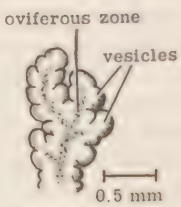

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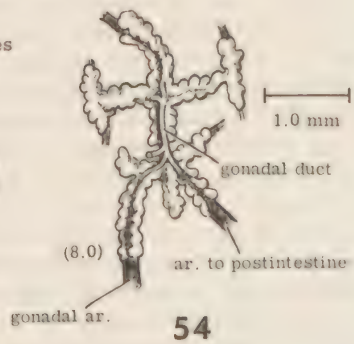

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male organs, and perhaps in the duct of the seminal receptacle. The musculature of the female tract is almost entirely circular, diagonal, or semispiral in character. The epithelium of practically every portion of the reproductive system seems to be glandular to an extent, except very notably that of the prostate pouch. Much of the gland tissue tends to have a semifluid, viscid consistency in life. The highly glandular uterus, which has minimal supporting tissue, superficially may seem to be hardly more than a turgidly swollen, weakly membranous bag, with semisolid contents when alive. With the slightest initial rupture of the wall - which occurs readily in dissection - the contents of the "bag" tend to burst outwardly, widely rupturing the wall. The other very glandular female organs are of similar consistency. When "well preserved," such organs are hard and brittle. In organs made up of minute, closely packed groups of glandular elements, such as the prostate, each group is evidently sheathed in its own extension of the general exterior strata of the tract. Accordingly, such organs have a complex skeleton of supporting tissue extending throughout their inner structure, which helps to make them much more solid and not noticeably semiliquid.

All of the reproductive organs are capable of at least slight, partially rhythmic, active contraction. Also, most or all of the narrow openings and ductal connections probably are capable of opening widely in normal functioning, at least passively. In life, the more muscular parts tend to be colorless, but glandular tissues are generally identifiable by their yellow to somewhat orange color. Some of the glandular organs are very bright in color, and particular tones and tints aid importantly in differentiating one from the other. In most specimens, black pigment occurs superficially throughout the genitalia as dusky flecks, which mostly are well dispersed so as to render the colors dull or grey in tone. Some individual snails have little or no such pigment. Cilia on the wall of the lumen form a generally uniform covering in nearly all parts of the female tract, even on the most glandular lamellae. They seem to be sparse, very small, or perhaps absent in the ovotestis, in most of the hermaphroditic duct, and in the prostatic region of the male tract. The cilia give off metallic, iridescent and golden reflections, by which their presence and distribution may be ascertained in dissection. Perhaps the cilia go through cycles of generation and regeneration in localized areas.

It is assumed here that the reproductive system of this snail is adapted to function regularly in both cross- and self-fertilization, and that there is physiological dominance of "crossing." Inseminating contact between sperm and ovum, in both selfing and crossing, must take place at the very beginning of the female tract, or in the hermaphroditic system, before the egg is enclosed in a "capsule." Therefore, if sperm placed in the vaginal region by a mating partner are to fertilize ova, they have to make the long journey to the very beginning of the female system; also, such sperm first probably have to "ripen" in the seminal receptacle, and this would necessitate a further journey, both ways, through the long receptacular duct. Moreover, the lumen of the female tract is highly occluded by lamellae or folds for most of its length at nearly all times, and commonly, if not always, it is blocked further by viscid secretions of those structures. A special pathway for "crossing," exogenous sperm evidently is provided for by what is here called the seminal gutter. This gutter consists of a uterovaginal and an oviducal division; it is somewhat interrupted as a morphological entity where the former gives way to the latter, and it is formed somewhat differently in the 2 divisions. It is prominently ciliated and is partly formed by a longitudinal excavation in the glandular epithelium, which causes a narrow longitudinal zone of the tract to be thin-walled. Externally, that zone is identifiable as the raphe. A longitudinal invagination of the wall of the tract at the edge of the raphe

forms a narrow fold which is placed so as to block off the gutter from the remainder of the lumen of the female parts. This mechanism of folding makes completely separate tubular tracts unnecessary for the oviposition and cross-insemination processes.

The bulkiness and complexity of the female tract reflects its major function of producing bulky and complexly structured egg masses. The egg masses are composed of mucilaginous material, and of egg capsules which are embedded in it. Each egg capsule contains an ovum or zygote suspended in a mass of nutritive syrupy liquid, the so-called albumen, which is shaped into a smoothly ovoid mass that holds its form by virtue of a delicate enclosing membranous coat. In the egg mass of the Houghton Lake population that coat is enclosed by up to 8 (but commonly several fewer) gelatinous coats shaped about it. The uncleaved ovum is ovoid-oblong, and about 0.14 mm in diameter; the egg capsule is 1 mm in length (or slightly more or less) and its gelatinous coats together are about 0.1 mm thick. Depending on factors such as those relating to physiological cycles, and the size, age, and health of the snail, the egg masses vary greatly in length and bulk. Anywhere from several to 100 (or perhaps more) capsules are arranged sequentially in the egg mass in a highly organized, partially multilinear, somewhat zigzag or slightly spiral, pattern. The capsules lie in a soft matrix which is sharply set off from a thick, firmly gelatinous multilayered wall which shapes and encloses it. A very flaccid but fairly extensive mucoid coat forms the outside of the mass. Transverse, semivertical, very delicate, membranous partitions occur in the matrix of the mass. The capsules are held in position partly by delicate "egg-strings," which attach to such partitions and other elements of the mass. The egg masses at their smallest are ovoid or short-oblong, but typical ones have the shape of a long sausage, except that they are flattened on the side by which they are attached to objects. Study of a great many egg masses taken in the field showed that those produced by the population under description were commonly 4 to 5 mm wide and 10 to 20 mm long, and that they ranged from 3 to 7 mm in width and up to 27 mm in length. An egg mass apparently is formed and deposited in a rapid sequence of processes. Later, sometimes within about 15 minutes, the ova may be seen to release polar bodies and begin cleaving. The major glandular organs of the female system must give up much of their substance in forming an egg mass, and they must transiently be much reduced in bulk in the process. The individual snail in Houghton Lake probably produces within the primary spring breeding season very many masses, of various sizes, in cycles, and it probably produces some occasionally at other times. Sampling data indicated that egg-laying in the population is largely suspended in early summer, resumed on a minor scale in midsummer, and suspended in late summer until the following spring. Phenotypic, individual variation in the size and appearance of the major glandular female organs may be much obscured by these circumstances. Note that the term "capsule" is used differently here than in certain literature, and that "ovum," as used here, may generally be interpreted as "primary oöcyte." Lymnaeid egg masses reportedly increase considerably in volume for some days after being deposited.

FIGURE 52. The same individual ovotestis as shown in Fig. 51, with its opposite, peripheral or abaxial face (the one directed away from the axis or columella of the shell) in view. In the natural position this face is embedded in the posterior liver, and several of its lobes penetrate to the abaxial surface of that organ. The tissues of the liver and its attendant vascular-connective complex (cf. Fig. 24) thoroughly ramify within, and fill the spaces between the shown lobes. Those tissues adhere intimately to the gonad, and can be removed en-

tirely only by picking them very carefully from the many crevices and minor depressions between and on the lobes. The gonad completely encloses a major arterial arborescence, around which it grows in its ontogeny (cf. Figs. 53 and 54). The 15 or so efferent vessels of the arborescence exit from the gonad by sharply defined cylindrical passageways, at the single or multiple tips of the major lobes and sublobes, of which there are also about 15. On exiting, these arteries plunge into and connect with the adjacent vascular-connective complex of the liver, except that the largest of these arteries (Fig. 48 and the following 2 figures) passes to the beginning of the postintestine. The gonads of no 2 individual snails are exactly alike in the number and form of the lobes, but 2 large anterior lobes, as shown, occur constantly. Every lobe consists of numerous capacious, branching tubes, which are walled internally with germinal tissue. The germinal tubes are walled externally by a membranous, tough tissue. They tend to be flattened and have scalloped edges due to an outpocketing of their sides which forms numerous close-set vesicles, arranged bilaterally in 2 series. The tubes mostly intertwine, although portions of some of them lie nearly parallel to each other, transverse to the axis of lobes of which they form a part. They are tightly bound together as if glued, so that they cannot be separated in dissection. Apparently the blind ends of most of the tubal branches lie on the gonadal surface, where their outlines can be made out only on close inspection. They hardly bulge from the organ and are flattened, so that in the mass they form a rather smooth surface. They could not be traced individually to demonstrate their full course or length, or the extent of their branching. However, they mostly did not seem to be many times longer than wide. In the base of each of the larger lobes there is a capacious cavity to which germinal tubes of the particular lobe evidently lead. An oval white parasite, about 0.3 mm long, with a pair of eyespots (an encysted mite?) occurred very commonly in the gonad of the snails in quantities sufficient to fill most of the gonadal lumen. Neither the figured gonad nor that of any fully adult specimen of the population seemed to be free of such infections. If the parasites caused gonadal damage, it was not apparent. However, it may be pertinent that in other populations of the *"L. emarginata"* type of snail, and in other forms of *L. catascopium* (*"L. elodes,"* etc.) the ovotestis generally was seen to be somewhat more loosely organized than that described here.

FIGURE 53. The gonad of an adult specimen, straightened out, and showing its adaxial face. This is a different example than shown in Fig. 52, but it is drawn to the same scale. The shown face is mostly not covered by liver tissue, and on it a low, roundly flattened elevation runs most of the length of the organ. The elevation fronts on a narrow portion of the visceral hemocoel which spirals along the axis of the shell, and it is part of a column, or main trunk, from which the gonadal lobes project. In substance, the column seems to be identical to the lobes in being composed of massed germinal tubes, which apparently lead toward the basal cavities of the various lobes. These cavities (perhaps 5) partly invade the column.

The ovotestis walls are rather transparent, and the internal contents readily show through them. At full maturity a diffuse zone of yellowish color courses along the inside walls of the germinal tubes and of their branches throughout the gonad. This zone at least in large part is confined to the more outward walls of the tubes and extensions of it are everywhere visible through the surface of the organ. Bright yellow ova (and nurse cells?) adhere to the tissue of this zone throughout its branching course, in a somewhat scattered arrangement. The

ova (and similar cells?), which possibly have amoeboid properties, were seen only in this oviferous zone, and may migrate to it as they mature. They apparently are so retained in the gonad until the formation of an egg mass is about to begin (cf. Fig. 57). Along with the ova, numerous deep orange and brown crystalloid granules of indeterminate shape and size also adhere to tissue of the yellow zone. In adults, apparently at all times and in all seasons, the germinal tubes as a whole are largely filled with sperm, which mostly occur in masses with their very long tails parallelly massed together. Many of the sperm are attached in dense clusters to the tube walls, in no apparent pattern, while many are free in the lumen. Masses of mature sperm are yellowish-white or of a creamy color, and somewhat iridescent.

In first-year snails which had attained a shell-length of about 8 mm, the ovotestis was entirely whitish, due to an internal accumulation of material which seemed to consist of sperm. Ova (or similar cells) were numerous in the oviferous zone in some first season (not overwintered) individuals of 11 mm shell-length, in which the ovotestis seemed to be filled with sperm. Colored granules first became noticeable in the oviferous zone when the snails reached a shell-length of about 16 mm, commonly in their first season. The granules appeared in greater numbers in older or larger snails, and in especially old snails they appeared free in numbers in the lumen of the germinal tubes, along with a thick yellow to orange fluid. In such specimens, sperm appeared in smaller volume and the number of ova in the oviferous zone was reduced. Adult overwintered snails almost always conspicuously showed the colored granules along with some colored fluid. In snails which were apparently stunted and aged, the deeper and darker gonadal colors were intensified and tended to replace extensively the lighter colors. The crystalloid granules and other colored material may represent germ-cell debris and their breakdown products, produced coincidental to oögenic and spermatogenic processes. Ovotestis parasites (cf. Fig. 52) perhaps affected some of the conditions noted here, but I could not detect any effect.

A thin-walled tubule, the gonadal duct, is embedded in a narrow longitudinal depression on the flattened face of the gonadal column. It is much narrower than the germinal tubes of the gonad. It is joined by at least 4 short tubules similar to it in diameter, 2 of which are shown in the figure meeting it at right angles. The tubules issue from membranous funnels arising in the gonad. The funnels are the outlets of the several spacious cavities in the gonad. The gonadal duct arises from a group of funnels in the apical region of the column of the ovotestis, and from a V-shaped juncture of a pair of ducts issuing from the 2 major anterior gonadal lobes. It is overgrown by membranous tissue of the gonadal column. The hermaphroditic duct arises from this duct as a tubule similar to it in diameter and appearance. This tubule forms a very short initial section of the hermaphroditic duct. The length of this section is exaggerated in the figure so that it may be indicated clearly.

FIGURE 54. A rough sketch of the ovotestis in an early stage of growth. A completely successful dissection of this stage was not made. At this stage the organ is about as long as the posterior liver, against which it lies in the spire of the snail. The branching nature of the germinal tubes is identifiable in dissection in some first-year specimens having a shell only about 4 mm long, in which the tubes are seen to be developing along the vessels of an arborescence of the gonadal artery, a branch of the major hepatic artery (cf. Fig. 48). The main branch of the gonadal artery then runs the length of the gonad. At the figured stage each branch of the gonad consists of a germinal tube which exhibits a longitudinal de-

pression accommodating an artery, and its scalloped sides have partly overgrown the arteries so as to invest them in places. Such investment leads to full enclosure of all adjacent parts of the arterial arborescence in snails that have reached a shell-length of about 11 mm. Evidently the tubes eventually branch profusely and irregularly, giving rise to successive series of branches. Possibly the anterior and posterior parts of the gonad are continuous with a single germinal tube which may connect them as a main trunk: however, it appears instead that there are at least 2 centers of development, of which a more posterior one may send out a germinal tube along the gonadal artery to an anterior center, where that tube becomes intergrown with tubes arising there. At the stage shown in the figure, the gonadal duct and its anterior bifurcation are clearly developed, as is the initial part of the hermaphroditic duct which issues from it. The indicated proportional relationship between diameters of the gonadal duct and the germinal tubes remains in the adult state. The gonadal duct possibly becomes established before any germinal tubes develop: it would appear that the ovotestis develops intially by growth of germinal tubes from the few extensions of the duct. The gonad takes on a lobate appearance resembling the adult condition in snails when they reach about 11 mm in shell-length.

FIGURE 55. Sketch of the blind branched end of one of the vesiculated germinal tubes which make up the ovotestis, as seen on the gonadal surface of an adult specimen (cf. Figs. 51-54). In young adults the structure shown is largely yellowish-white due to masses of sperm showing through its wall; the indicated zone is internal and is formed in and on the germinal tissue: it is flecked with orange and brown granules and conspicuously highlighted by bright yellow ova, (and perhaps "nurse" cells), scattered along it. Portions of this oviferous zone in many such germinal tubes combine to create a mottled and reticulate color pattern in all regions of the ovotestis. The face opposite that shown is smooth and lacks the colored zone. Note that such tubes strongly tend to be bilateral in symmetry, and resemble the main division of the hermaphroditic duct in structure (cf. Figs. 51 and 56).

FIGURE 56. The hermaphroditic duct of 3 adult specimens. The organ has 3 definable divisions: a minute initial stalk, which connects with the gonadal duct, a broad vesiculate one, and a narrow terminal one. The vesiculate division makes up most of the organ and it functions as one large seminal storage chamber or "vesicle" which is practically sessile on the gonadal duct (Fig. 53). Cilia were not detected in this division or the preceding stalk. Fine, musculoid elements are faintly seen on its outer surface in dissection. The vesiculate division consists only of a thin, slightly fleshy wall which is dusted with granules of dark pigment, and its seeming bulkiness, indicated in the drawings, is due to sperm within it. The sperm form one continuous dense, cottony, firm mass of an opaque yellowish-white to slightly pink color, which extends from one end to the other of the division, and fills the many vesicles protruding from it. Within that mass the sperm tails are mostly parallelly contiguous with each other within large swirled bundles, which are partly intertwined with similar bundles. Not rarely, the tissue of the bulging end of many of the vesicles is pale orange or brownish. It is suspected that this is indicative of a "sperm-ingesting" function (cf. Fig. 78). In many hundreds of dissections of specimens collected in all seasons, ova were never seen in the hermaphroditic duct.

The hermaphroditic duct develops early in the life of the snail: it was detected in a specimen only 7.6 mm in shell-length, as a narrow, straight white tube, which

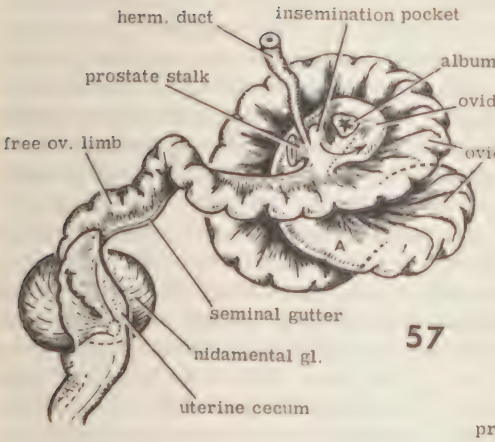
had fine vesicles arranged in 2 bilateral series. In some specimens having shells only 8 mm long, the duct was decidedly vesiculate, somewhat contorted, and solidly packed with plain white sperm-like matter. The turgid condition of the duct and color of the sperm mass characteristic of the adult state appears in some first-season specimens having a shell only about 10 mm in length. In immature stages the main division of the duct is rather flat and clearly has a bilateral symmetry; a smooth semicylindrical elevation runs its length, down the center of one of its faces, between the 2 rows of vesicles. The vesicles encroach on the opposite face and fuse with, or interdigitate with, vesicles of the opposite series, across this face. In the younger stages the vesicles are fairly regular in size and alignment, and those of one series may tend to be paired with those of the opposite series. However, there is always some irregularity. Some vesicles are notably larger than adjacent ones. They may be irregularly out-pocketed themselves, and some are crowded out of line in the series. The vesicles are rounded and mostly shaped like a kernel of maize; some may tend to be angular, but they are not pointed or strongly angular as in certain other lymnaeid species. Irregularities among the vesicles are enhanced in larger, older snails, in which sperm are found stored in large volume; then, the vesiculate division of the duct characteristically is kinky and contorted, and some of the vesicles, singly or in groups, are excessively expanded. When carrying its greatest sperm load the major division is especially expanded in its posterior end, as in the drawing on the right. In this condition, the vesicles encroach greatly on both of its faces. The condition of the duct routinely seen in hundreds of specimens at most times of the year was almost always much like that shown in the middle drawing. The especially swollen state as shown on the right was particularly noted in larger first year specimens shortly before the winter season and in specimens taken from under the ice in the winter.

Most of hundreds of specimens collected in April and May showed the reduced condition indicated on the left. This circumstance coincided with the finding of vast numbers of egg masses in the habitat (cf. Fig. 1). The hermaphroditic duct then was especially reduced in the breadth of the posterior end of its main division, its vesicles were reduced in size and number, and its kinks and contortions were largely eliminated. Also, it was short, thick-walled, and pigmented to an extent which at first seemed quite abnormal. The posterior end of the duct was particularly heavily pigmented and quite blackish. These observations, with further information obtained (cf. Fig. 1), seem to indicate that most of the snails of the Houghton Lake population accumulate a store of sperm in the summer and fall of their first year, and that they largely expend it in a highly limited mating season very early in their second year, in close chronological connection with melting of the habitat's ice cover, and with a highly limited egg-laying season. After release of most of the stored sperm, there is actually retrogressive growth in the length of the hermaphroditic duct, by reduction of the length of the vesiculate division. The wall of this division, which is very elastic and usually stretched very thinly at other times by sperm masses, then contracts and "thickens up" considerably. The pigment granules on its walls are dispersed widely when the wall is stretched, so that it is but faintly dusky; the pigment becomes concentrated with contraction of the wall, resulting in a marked darkening of the tissue. In many specimens exhibiting this reduced condition, a deep orange-yellow, thick fluid was present in the posterior reduced portion of the broad division of the duct. Such material was never otherwise seen in the duct. It seems that after a snail's first mating season, sperm are usually accumulated in its duct until the next year's mating season, and that the hermaphroditic

duct, by regrowth, re-elongates and develops additional vesicles in response to the "storage demand" placed on it. Mating evidently occurs occasionally outside the spring season (cf. Figs. 77 and 78). A few snails among those collected in the summer, fall and winter showed the reduced "post-mating" condition of their hermaphroditic duct. Data related to this suggests that the hermaphroditic sperm reservoir usually may not be emptied of most of its contents in a single mating, but rather emptied when a snail mates as a male especially frequently, or exhaustively, during a short period of time.

The anterior terminal division of the hermaphroditic duct is narrow and of consistent length. It regularly shows a kink near its mid-length, and it is often finely pustulate in its posterior half. It seems to have a ciliated lumen that is very narrow at almost all times. Its wall is of tough consistency and shows some circular musculature. In one dissection it was found to be much expanded at its terminus, and in widely open communication with the male tract and the insemination pocket.

FIGURE 57. The carrefour complex and adjacent portions of the oviducal and uterine divisions of the reproductive system, drawn slightly stylized. In nature, the shown surfaces of the oviducal cecum and adjacent structures are closely adherent to and hidden by the albumen gland, which has been removed in the figure. The shown portions of the hermaphroditic and male tracts and of the duct of the albumen gland, which are indicated as severed, are considered to be part of the carrefour mechanism, along with the insemination pocket, the oviducal cecum, and the labyrinth. Since the word "carrefour" refers to a juncture of pathways it is not applied to a particular organ. The insemination pocket morphologically and functionally is the initial element of the female tract, and here it is considered to be one of the elaborations of the oviduct, which include the cecum and labyrinth. The labyrinth is not a tubular structure, as it appears to be on superficial inspection. It is difficult to describe but it may be visualized roughly as a compressed discoidal sac, which is suspended from the origin of the oviduct, and partly twisted and folded upon itself. Internally, its twist forms an incomplete sort of "columella." The ruffled border of the labyrinthal loops is thickened and highly glandular; the lumen in it is continuous along its length with the narrow and twisted axial lumen central to it, which is roofed and floored throughout by thinner glandular walls. Morphologically, the peripheral lumen forms a looped, semitubular tract, both ends of which are produced as tubular extensions, which are the oviducal cecum and the free oviducal limb. The latter is quite like the major loops of the labyrinth in glandularity and appearance. The former is much less glandular, rather thin-walled and smooth, as is the initial part of the first loop (to point A). The oviducal cecum leads directly into the initial part of the labyrinth, and functionally it immediately succeeds the insemination pocket. The albumen gland duct opens directly into the cecum by a large slit, bordered by prominent fleshy-glandular lips. The axial lumen of the labyrinth is traceable to the oviducal cecum through a twisted crevice-like passageway where it is blocked by a fold that is an extension of one of the lips at the outlet of the albumen gland duct (cf, Fig. 62). The edge of this lip-fold is indicated in the figure by a dotted line, as if it were visible through the cecal wall. This fold prevents open communication between the insemination pocket and the axial portion of the labyrinthal lumen, while leaving a broad but flattened passageway between the pocket and the oviducal cecum. Both ends of the long semitubular peripheral labyrinthal tract are brought by their looped arrangement almost to the same point in proxim-



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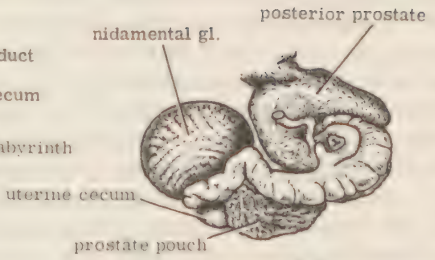

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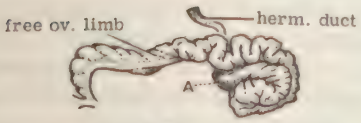

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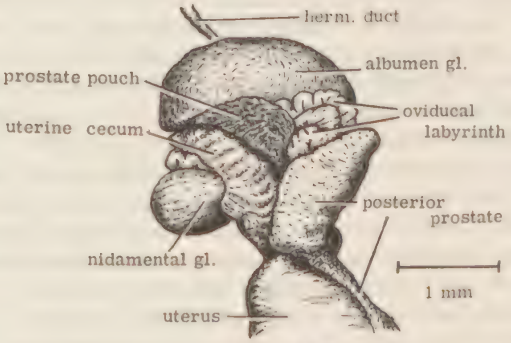

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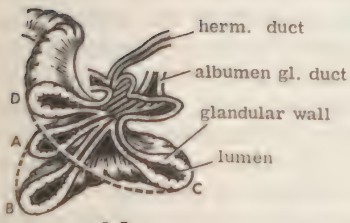

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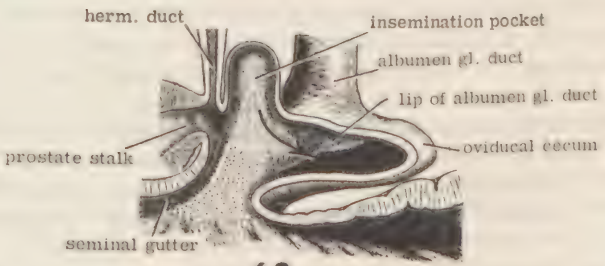

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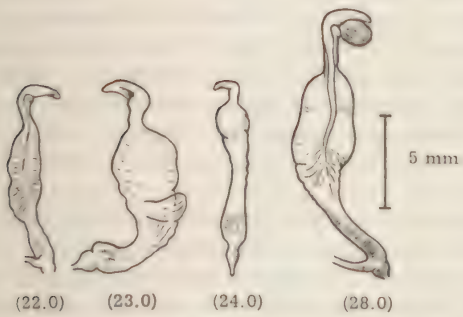

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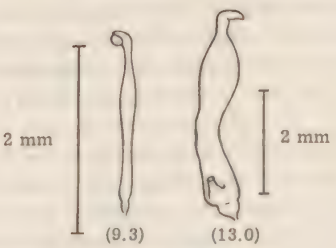

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ity to the insemination pocket. As an adaptation, this seeming peculiarity has permitted adding greatly to the effective functional length of the female tract without adding to the length and complexities of the journey which exogenous sperm must make to achieve insemination. It allows the seminal gutter to bypass the labyrinth while leading directly to an insemination site at the entrance to the female tract. The oviducal division of the seminal gutter is formed in the flattened, keeled margin of the oviducal free limb, in which it is set off by a linear invagination corresponding to the fine dashed line in the figure (cf. Fig. 74). It begins at the tapered terminus of the oviducal limb, which opens into the cecum of the uterine division of the female system. The terminal portion of the oviducal tract is tightly sandwiched between the uterine cecum and the nidamental gland. The nidamental gland arises by a stalk from the end of the oviducal tract and adjacent tissue of the uterine cecum. That gland may be classified somewhat arbitrarily as an oviducal organ. The cecum is a blind, reverse, direct extension of the uterine tract. The oviducal tract then can be said to terminate on the side of the posterior end of the latter tract. Perhaps the uterine cecum serves in part as an accessory seminal receptacle - a way-station in the journey of sperm from the vagina to the site of insemination. If so, this might make a store of exogenous sperm more immediately available when insemination is about to begin.

The seminal gutter ends in immediate proximity to the outlet of the hermaphroditic duct, and at its entrance into the male system as well (cf. Fig. 62). Perhaps nothing prevents sperm from passing from the gutter into either of those openings, or from them into the gutter. In one dissection, the end of the hermaphroditic duct was found gaping widely and simultaneously into the insemination pocket and the male tract. Therefore, the possibility exists that a mixture of selfing and crossing sperm may occur at various points in the hermaphroditic and female systems, perhaps even in the seminal receptacle. This perhaps might mean that one snail could fertilize another snail with yet a third snail's sperm. On consideration of the structures demonstrated here, and of published knowledge of egg masses (cf. Fig. 51) and of reproduction processes in lymnaeids, it is suggested that the following sequence of processes occurs in the figured region of the present species, upon initiation of the oviposition activity. The ova may be delivered to the insemination pocket singly in rather rapid sequence from the hermaphroditic duct, each ovum perhaps with a small amount of sperm. If that sperm is not already a selfing and crossing mixture, it could become so in the pocket if exogenous sperm is delivered there simultaneously from the seminal gutter. It is assumed that in such mixtures, endogenous sperm could not "compete" successfully with exogenous sperm, and would fail to fertilize in their presence. The ova probably are actually fertilized after they leave the insemination pocket, the function of which may be to insure that a regulated quantity of sperm is delivered to, and molded to, each of the ova in succession (small quantities of sperm are frequently to be seen within the egg capsules; also, cf. Fig. 51 as to evidence of delayed fertilization). As indicated by the arrow in the figure, it seems that each packet formed of one ovum and a batch of sperm would be carried from the pocket by ciliary action across the lip of the albumen gland duct and into the oviducal cecum, where it would be flooded by albumen. The amount of albumen supplied to each egg perhaps is controlled by the lips of the albumen gland duct. Perhaps albumen accumulates in the duct while the lips are closed, until the standard amount can be released by opening of the lips. The oviducal cecum probably molds the albumen about the ovum and its sperm, and it may add the membranous coat which finally encloses the whole. The so-formed ovoid body would then pass into the semitubular peripheral tract of the labyrinth (to and then past point A), and then move along all the labyrinthal loops; it then

would pass into the free oviducal limb. In this course, in passing from one "ruffle" to another, the capsule probably receives its series of gelatinous coats, and perhaps some "strings," and thereby it would become completed. During its formation, probably a number of other capsules are being formed while moving along, single file, in the labyrinth. On completion, the capsules proabably file one by one into the uterine cecum from the oviducal limb. If endogenous and exogenous sperm are not mixed in the hermaphroditic system, then it would seem that while egg capsules are descending in a series down the free limb of the oviduct, a stream of sperm (in packets?) is also rapidly ascending that limb in the opposite direction, from the uterine cecum. It would be important that this division of the gutter is then open where it leads from the uterine cecum. Note, then, that the oviducal outlet is toward the rapheal side (cf. Fig. 68) of the uterine cecum and how (cf. Fig. 69) it faces directly toward that side by the exact way it is positioned in the cecal wall. Also, note how the oviducal division of the seminal gutter arises toward the same side. This arrangement must help to insure that sperm in the cecum have access to the oviducal limb while ova are being inseminated in rapid succession, even while quantities of matrix-jelly are being extruded into the cecum through the oviducal outlet. The uterine cecum may provide the mechanism which arranges the eggs in an organized pattern in the matrix of the egg mass. The matrix undoubtedly is supplied by the nidamental gland, which might then best be called "the matrix gland." The arrangement of the parts suggests that capsules individually may establish connections with portions of the matrix as they pass by and against the outlet of the gland. Both muscular and ciliary action are probably necessary to the structuring and molding of the egg capsules, and in moving them along the oviducal tract. In physiological salt solution, the oviducal structures, as a whole, show pulsatory, simultaneous, infrequent movements. In the free limb, the pronounced peristaltic waves of contraction are to be seen moving toward the uterine cecum. The oviducal tract and its extensions are generally markedly ciliated, except in a particular area noted in reference to Fig. 62.

FIGURE 58. The carrefour complex in its natural position in relation to adjacent reproductive structures and oriented as in the preceding figure, with the albumen gland similarly eliminated. This is a precise scale drawing representing the same specimen, to the same scale, as is shown in Figs. 59 and 60. Organs of the same individual snail also are represented in Figs. 63 and 65-68, on different scales. The part of the posterior prostate shown looks somewhat broader and more massive in this view than it really is because it is somewhat twisted and folded up against the labyrinth (cf. Fig. 79). Note that the prostate pouch passes "under" one side of the oviducal limb, and that it is so curved that the edge of its broad end tends to overlap the edge of the opposite side of a succeeding part of that limb. This arrangement is constant from specimen to specimen. The tip of the uterine cecum is visible near the end of the prostate pouch.

FIGURE 59. The oviducal division of the female tract dissected free from adjacent structures and oriented almost exactly as in the following figure. That figure and Fig. 58 represent the same individual specimen. Point A corresponds to point A in Figs. 57 and 61. The labyrinthal tract between the oviducal cecum and that point tends to be darkly pigmented, which may be indicative of special vascularization.

FIGURE 60. The adult carrefour complex, in its natural positional relationship to adjacent reproductive structures, together with which it forms a compact, highly glandular mass, the dorsal aspect of which is shown (cf. Fig. 2). The labyrinth and the adjacent part of the oviducal limb (cf. Figs. 58 and 59) are tightly sandwiched between the albumen gland and the posterior prostate. The lines of separation between the organs, and between loops of the labyrinth, can be very difficult to trace, partly because the entire organ-complex tends to become uniformly greyish-white in preservative and partly because it has a peculiar consistency, when alive or preserved, which prevents probing it successfully. The difficulty is enhanced because the organs are tightly bound together by fine, abundant, membranofibrous elements. In certain preserved states the substance of the different organs tends to intermingle and fuse to a degree at various points, because of partial breakdown of tissues. If "well-preserved," the mass of organs tends to be hard and brittle, and when probed or cut it commonly fragments, even across the lines separating its parts, so that chunks which break off may consist of parts of 2 or more organs. When under-preserved, the organs of the complex become mushy or gelatinous and the cohesiveness of their primary substance becomes less than that of tissues which bind them together. When alive, the organ-complex is difficult to dissect successfully because of its overall lack of solidity, and the delicacy of the supporting tissues.

All of the organs in life are translucent to a degree but the albumen gland and posterior prostate are more opaque, more light-reflective and brighter, and more solid in substance than the labyrinth and free oviduct. The albumen gland usually is uniformly orange. The posterior prostate is similar to this gland in color, but it is generally more yellowish and more opaque. In life, the labyrinth is quite translucent, and has a milky to yellow-cream general reflectivity, while the free oviducal limb looks identical in these respects. The intensity of the colors of the organs probably relates to cyclic changes relating to function. Dusky pigment finely flecks the surfaces shown, and is concentrated on the prostate pouch. The pouch is very dusky or blackish, and thereby it usually stands out visually among the organs. The prostate pouch also contrasts in its nature with the other organs in having a very thin wall (cf. Figs. 74 and 79). It is not exposed on the face of the mass opposite to that shown. Note that the pouch and the posterior prostate, in combination, wrap almost entirely around the base of the labyrinth. The uterine cecum shows a series of wrinkles on the particular side in view. This wrinkling is enhanced in strong preservative, but it is hardly noticeable in "fresh" material; it reflects an internal structural arrangement, which may be significant in egg-mass formation (cf. Fig. 65).

FIGURE 61. The carrefour complex, represented somewhat stereogrammatically to clarify its basic structure (cf. Fig. 57). Portions of the labyrinthal loops are shown cut away; their course is indicated by dashed lines. Letters A to D indicate the order of morphological succession of portions of the loops as well as the sequential positions which the egg capsules may theoretically occupy as they are being formed. The labyrinthal tract begins while leading directly from the oviducal cecum to point A. The area ruled in white represents a continuous surface formed by one wall of the insemination chamber, by a lip fold of the albumen gland duct and by one wall of the labyrinthal loop between C and D (cf. Fig. 62). That surface is incompletely represented in order not to obscure the fact that axial communication exists between all of the labyrinthal loops.

FIGURE 62. The insemination pocket, in relation to other structures at the beginning of the male and female systems. The walls which would be nearest the viewer have been removed to show internal relationships. The opening into the prostate stalk at nearly all times appears to be a slit (cut through vertically here), which is perhaps too narrow to allow ova to pass into it. Ciliary control also ordinarily may insure that ova regularly bypass the entrance into the male system. In this region, the seminal gutter is very heavily ciliated and it leads directly to the base of the insemination pocket. The end of the hermaphroditic duct seems to be ciliated. The insemination pocket is densely ciliated, as is the lip of the albumen gland duct shown. Cilia were not detected with certainty in the prostate stalk. The arrow indicates the path the ovum apparently must normally follow after it receives its inseminating sperm in the pocket. However, there is evidence (cf. Fig. 78) that sometimes, and perhaps not rarely, ova may pass back across this region from the uterine cecum (reverse to the arrow) into the male tract after they are enclosed in albumen and its membranous coat. Perhaps this inadvertently happens when the snail is forced to retract violently into its shell during egg-capsule formation. The stippling indicates an area in which cilia seem to be absent. Against this area the opposite wall (cut away), which is somewhat toughened, normally is rather closely appressed. This area seems to be a blocking mechanism which ordinarily prevents ova from passing directly into the free oviducal limb from the insemination pocket. Note how the overall mechanism seems to insure that the ovum is positioned to be flooded with albumen immediately after it receives its sperm. The oviducal cecum is smooth-walled and is well-ciliated throughout. There is a second lip of the albumen gland duct, which is hidden in this view by the lip shown. These lips are continuous with each other around the basal edge of the duct on the right in the figure, and so form a "U." The hidden lip extends some distance into the axial region of the first loop of the labyrinth. The albumen gland duct internally is heavily, longitudinally plicate. Its base tends to be inflated; perhaps this relates to regulating the quantity of albumen delivered to each ovum as capsule formation begins.

FIGURE 63. Four examples of the uterovaginal division of the female tract, illustrating variation in adult snails. All are drawn to the given scale. The first 3 preparations from the left are preserved. The primarily oviducal organ, the nidamental gland, is shown in its natural position against the uterine cecum, in the largest example. The third example from the left is the same individual organ shown in Fig. 66; it and 2 of the others shown have been forcibly straightened out for purposes of measurement. The second example from the left exhibits the natural posture as observed in well-expanded snails. The illustrated variation is the sort seen in population samples taken in all seasons (note the indicated shell-lengths). To some extent it may reflect really phenotypic individual differences, but it largely expresses the effects of functional activities, of preservation, and of factors relating to health of the individuals. In oviposition (cf. Figs. 51, 57 and 66) the main glandular organs must give up much of their substance to the egg mass that is formed. Accordingly, observed great variations in the robustness of those organs may be transient, and closely dependent on oviposition cycles. The third preparation from the left illustrates effects of trematode infections. The parts apparently were arrested in growth before they reached the fully adult condition. As a result this division of the tract has a juvenile appearance despite the large-adult size of the snail (cf. Fig. 64). In this case only traces of the parasites were found in the snail, along with minor evidence of their other pathological effects. Evidently, a minor infection had existed, and the parasites almost en-

tirely were shed from the snail before it was collected. This infection probably was acquired, or matured, fairly early in the life of that individual. The first example from the left represents a condition which is believed to follow upon laying of an egg mass (cf. Fig. 66). It appears as if it had undergone retrogressive growth, but note that the uterine cecum is of adult size. It has a coarse aspect, it is reduced in bulk and dimensions, and its dusky pigmentation is enhanced by being concentrated within a reduced volume and area. It is believed that such an appearance is also the characteristic result of infections which are acquired, or which mature, late in the life of a snail, and cause atrophy of the uterus and other major glandular organs. The second and last drawings from the left show variants found in healthy adults. The former illustrates a "rugged" appearance which is associated with "overpreservation," and the latter represents an unpreserved specimen killed by drowning, in which a smoothness of outline characteristic of unpreserved organs is evident. In the latter example, the shown divisions of the tract are the longest and largest ever seen in the population. It was from the largest snail dissected. While it represents a normal, approximately maximal development, drowning seems to have contributed to the unusual dimensions. In this case, the provagina is quite cylindrical, a condition rarely seen among the snails; it also is very unusually firm and thick-walled, and looks muscular to a very unusual degree. These appearances are not individualistic but result from constriction of the tract by the contraction and "condensation" of more or less circular muscle elements in the provaginal wall (cf. Fig. 66). In this state, the inner provaginal wall is elevated into large, crowded plicae. The provagina is capable of remarkably great dilatation, when its wall is exceedingly thin, delicate, and seemingly non-plicate. The second drawing from the left illustrates the curvatures, conformity and relative dimensions of the parts when the uterovaginal tract is in its resting state. It may be taken as a demonstration of the primary, fundamental, or intrinsic form of the provagina, which seems to be markedly constant in actuality. The terminal broadening and the elbowing of that organ were often seen in the population, exactly as shown. In this condition the provaginal wall is moderately thick and looks moderately muscular, while the organ itself is flattened ventrally, especially toward its terminus. The beginning or posterior end of the provagina, which is weakly muscular, tends to form a broad "cowl" outward to its elbowed side, which in the resting position is cupped around the left anterodorsal side of the uterus.

In life, the main uterine body has a deep yellow to orange-yellow color in the robust adult state. The color may be intense and bright, but it tends to be dulled by faint dusky flecking and a greenish cast relating to the general translucency of the organ. The non-rapheal portions of the uterine neck are essentially identical in translucency and color. The raphe is transparent to opaque, and pearly-whitish; it is greyed by a general abundance of dusky flecking on its outer surface, while a violet iridescence of its inner wall is commonly visible externally. These appearances extend to the rapheal part of the uterine cecum, and make the course and extent of the corresponding seminal gutter rather easily traceable on the exterior of the tract. Yellow and orange tones extend into the non-rapheal side of the uterine cecum and into the vaginal region. On a number of folds forming V's (indicated in the far-right drawing) at the ventral posterior end of the provagina, the yellow color often is more opaque and intense than elsewhere in the tract, and even brilliant. In the terminal half of the provagina such colors give way to paler, more whitish tones. Usually, the provagina is greyed generally by relatively abundant dusky flecking which in part is linearly con-

centrated so as to delineate the internal folds of the organ. The more that organ is constricted, the more the dusky flecks are concentrated, and when highly constricted it tends to be nearly black.

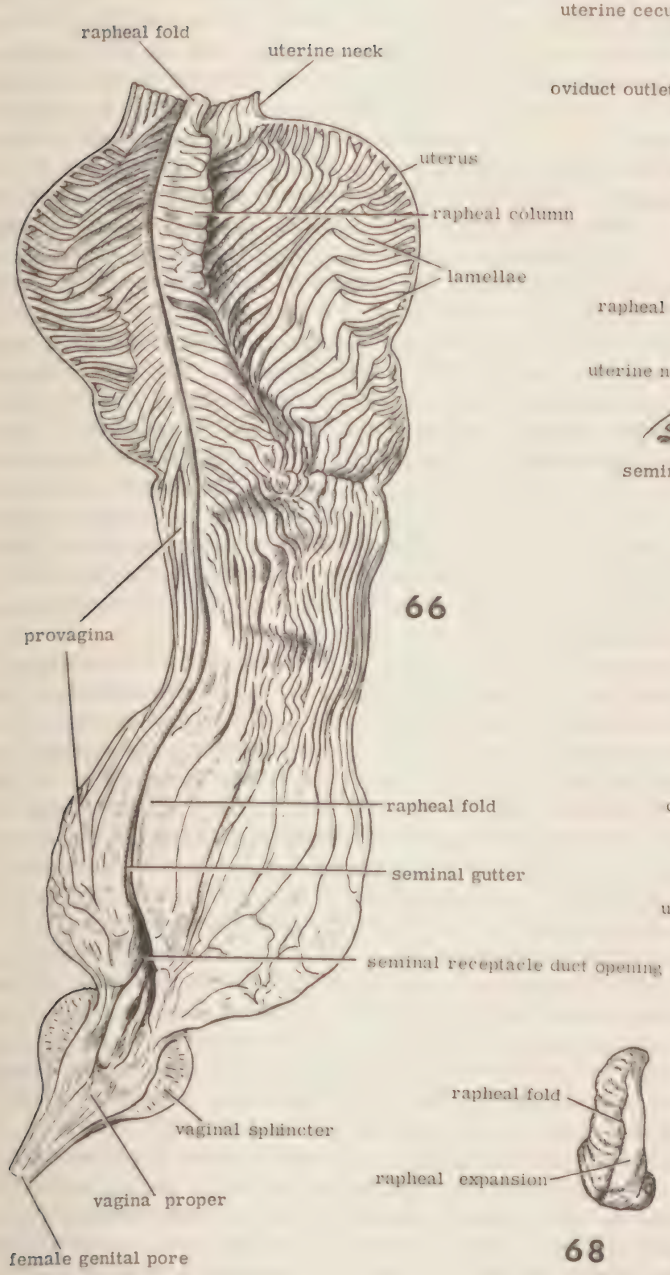
FIGURE 64. The uterovaginal division of the female tract of 2 immature specimens, indicating ontogenetic stages. The smaller drawing illustrates the fact that by the time many snails of the population reach a shell-length of 10 mm, they have developed as morphological entities the nidamental gland and the cecum, the neck and main body of the uterus, as well as the provagina, vagina and vaginal sphincter. Note that this division of the tract may closely approach the adult condition in shape and proportions of its parts before a shell-length of 15 mm is reached. Note especially that the intrinsic form of the vaginal region characteristic of the population begins to become evident at a very early stage of development (cf. Fig. 63, second drawing from the left). In the later stage shown the raphe (cf. Fig. 63) can be traced, but it is difficult to see. In the earlier stage figured the organs are entirely milky-white and almost opaque. In the other stage, the form, color, translucency and glandularity characteristic of the adult have begun to be evident.

FIGURE 65. The uterine cecum and the uterine neck, with their walls opposite the raphe cut open longitudinally and spread open. The cecum has been disconnected from the preceding oviducal tract and its nidamental gland. The rapheal fold extends into the cecum almost to its tip, as a pronounced entity (cf. Fig. 68) although this not evident in the figure. It has been pulled to the right, along with the rapheal fold in the neck and along with the rapheal column. In their natural position these successive structures fit over the seminal gutter (cf. the cross section in Fig. 69). Then they block off the space in the gutter from the remainder of the lumen in the cecum, in conjunction with a smaller parallel fold in the neck. The gutter expansion may function as a seminal reservoir (cf. Fig. 57). It corresponds with the externally defined rapheal expansion (cf. Figs. 51 and 68). The walls of the cecum and neck are well ciliated; the non-rapheal portions are highly glandular overall, and abundantly invaginated so as to form the indicated folds and clefts. The clefts are mostly deeper than would appear from the figure. The wall of the seminal gutter and its expansion is much thinner, much less glandular, and more heavily ciliated than the adjacent walls. Note that the linear fold on the left edge of the gutter leads to the oviducal outlet, but that the uterine division of the gutter ends with its cecal expansion. Sperm in the gutter expansion would have access to the adjacent oviducal division of the gutter through the oviducal outlet indicated. This outlet is not only generally narrow, but always seems to be quite occluded by the thickly glandular substance of both the stalk of the nidamental gland and the end of the oviduct. Perhaps sperm enter the oviducal gutter only in very small numbers, maybe in packets, or perhaps the oviducal outlet opens widely at times and permits their passage in quantity. In the process of egg-mass formation the oviducal outlet must open to a diameter of at least 1 mm to allow passage of egg-capsules. In the oviposition process the non-rapheal portion of the cecal lumen set off by the rapheal fold may serve as a molding chamber for the capsular matrix of the egg mass supplied by the nidamental gland. This gland's secretion issues into the cecum by the indicated oviducal outlet.

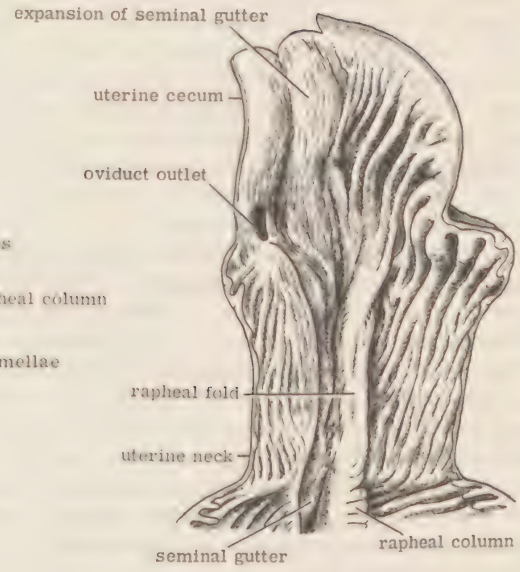
The folds in the uterine neck project bulbously into the lumen of the tract at the base of the cecum. They evidently can be crowded together by muscular action so as to block completely the exit from the cecum. Probably this aids in

shaping the initial portion, or leading end, of the capsular matrix. This end would pass thereafter into the neck, upon retraction or depression of the folds of the neck. As this end moved onward, the forming matrix-body would be built up by additions to its trailing end. Fluid pressure from the rear, muscular contractions of the neck, and ciliary action all could contribute to molding the matrix and moving it toward the following main body of the uterus. Meanwhile, the walls of the neck also probably form the initial layer of the firm gelatinous wall which encloses the soft matrix in the completed mass. The arrangement of the capsules in the matrix perhaps is controlled largely by folds in the cecum. The clefts between the folds can take on the appearance of a series of rather capacious pockets. These correspond to swellings on the outer non-rapheal surface of the cecum (cf. Fig. 68). Perhaps capsules accumulate in the cecum in small numbers and then become arranged simultaneously in individual pockets; perhaps the formation of membranous partitions of the matrix and the anchorage of eggs to them takes place at that time. By such means, capsules may become incorporated as organized groups into successive portions of the matrix. In these processes the rapheal fold possibly does not effectively block off the seminal gutter entirely. If the organs become considerably distended in such activities, the rapheal fold along with the other folds might spread apart and flatten out so as to expose the gutter. In the neck, fine musculo-fibrous elements, arranged so as to act as constrictors of the tract and as retractor-depressors of the folds, are especially abundant. In physiological salt solution the neck shows occasional pronounced contractions. Stimulation of the base of the uterine cecum with a probe sets off a decided peristaltic wave, after a considerable time-lag, along the uterine neck to the main body of the uterus.

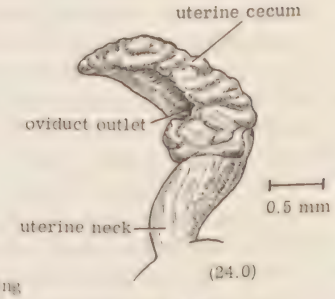
FIGURE 66. The uterovaginal tract with its uterine neck and cecum removed. It is shown slit open longitudinally on the dorsal side and spread out. As a rule, it is impossible to make such a preparation of a completely normal adult specimen, alive or preserved, because the semi-gelatinous (when alive) or brittle (when preserved) nature of the uterine structures prevents successful manipulation of the organs (cf. Figs. 51 and 60). The preparation figured is of a pliable consistency because of the combined effects of an accident of preservation, and a minor trematode infection (the same individual specimen is represented in Fig. 63, by the third drawing from the left. The preparation had been allowed to macerate after being "overpreserved." Its parts are smaller, and its main uterine body is of less mucoid-glandular texture than those of normal adults preserved the usual way (in healthy juveniles and subadults the organs tend toward this same condition). Repeated examinations of normal specimens showed that this preparation is otherwise quite normal in the essential features figured. The main uterine body exhibits only exceedingly delicate muscularity (cf. Fig. 51). It is largely composed of numerous lamellae, each of which consists of 2 thick ciliated strata of high-columnar gland cells and a supportive, dusky, double-walled membrane which separates those strata. The gross histology and primary structural features of the lamellae are the same as in those of the nidamental gland (cf. Fig. 74). On all of the cut lamellar edges shown, the double membranes are visible in dissection as a dark line running down the center of the cut surfaces, but this is not indicated in the figure. The lamellae represent very deep invaginations of the uterine wall and their internal membranes are continuous with musculomembranous tissue which form a delicate "skin" over the entire uterus. On the outer surface of the uterus the position and course of each lamella is marked by a dusky line, which represents the line of invagination. The number of the


rapheal fold
uterine neck
uterus
rapheal column
lamellae
provagina
rapheal fold
seminal gutter
seminal receptacle duct opening
vaginal sphincter
vagina proper
female genital pore

66


expansion of seminal gutter
uterine cecum
oviduct outlet
rapheal fold
uterine neck
seminal gutter
rapheal column

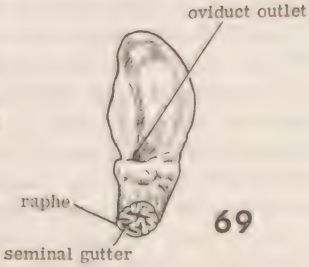
65


uterine cecum
oviduct outlet
0.5 mm
uterine neck
(24.0)

67

rapheal fold
rapheal expansion

68


oviduct outlet
raphe
seminal gutter

69

lamellae seems to be established early in ontogenetic development and it does not seem to change with age.

The indicated rapheal column is built up of a series of blocky structures quite like the primary uterine lamellae in character. This series arises from, or is set on, a flap of tissue (an invagination of the uterine wall) which runs longitudinally in the uterus and with which it is morphologically united. In the natural position, the column is folded over toward the right side of the uterus (to the left in the figure) so that it lies directly over the seminal gutter and roofs it. In the figure, the column has been lifted up and pulled a bit toward the right of the figure, so as to reveal the edge of the seminal gutter. This has brought the flattened right side of the rapheal column upward and into full view. In its normal position the right edge of the column lies against a flat longitudinal strip of gland tissue which borders, and is elevated above, the right edge of the gutter. This strip is built up against a minor longitudinal invagination of the uterine wall. The lamellae of the uterus arise from this strip, as low, flat plicae. From there they pass circumferentially on the walls of the uterus, from the right and to the left, where they end in a longitudinal crevice (an angular trough in the spread-open preparation) formed by the juncture of the left side of the rapheal column with the uterine wall. In their course, which is mostly semi-spiral and diagonal to the uterine axis, the lamellae become very broad and shelf-like, and then become reduced to small tapered plicae. Tapering to an end, they meet with similar tapered ends of the lamellar elements of the column in the longitudinal crevice. The lumen of the uterus is almost completely occluded by the column and lamellae. The lamellae, as a body, fit about the column closely, and thereby set off a longitudinal division of the lumen which in cross-section is C-shaped. The open side of the "C" is ventral, and the column, in section, fills the "C."

As the uterine lamellae descend into the crevice beside the rapheal column and diminish in size, they angle or curve toward the anterior end of the uterus. The lamellar elements of the column also diminish and point anteriorad as they descend in the crevice, at the bottom of which they meet the ends of the other lamellae, and partly coalesce with them, forming some V-shaped junctures. In the crevice the points of the V's and the ends of numbers of lamellae are extended as low longitudinal linear plicae, which course in the crevice toward the anterior end of the uterus. In the anterior end of the uterus, around the periphery of its wall, similar plicae arise from lamellae. The rapheal column, in proceeding to the provagina, broadens and becomes lower, and then becomes obsolete by merging into the general topography of the walls of the tract. Further linear plicae arise from the lamellar elements of the column as it loses its identity. As such plicae arise from various points they mostly become closely parallel to each other, and they pass into the provagina, where some of them branch and make diagonal interconnections. Thereby the wall of the first half of the provagina takes on an overall longitudinally corrugated appearance. The plicae and their separating clefts have a substantial ciliated glandular epithelium which is an extension of the uterine epithelium. The clefts are mostly sharply defined and deeper than is evident from the figure. Also not evident from the figure is the fact that the anterior, following half of the provagina bears many, though fewer, plicae which may be quite high and coarse when elevated. When that region of the tract is especially narrowed by its constricting musculature (cf. Fig. 63) these folds are markedly elevated and largely occlude the lumen (a cross-section of the constricted provagina would greatly resemble the cross-section of the rectum shown in Fig. 22). In this figure, the folds are retracted and depressed, and nearly obliterated. Particularly pronounced retractor-depressor fibers insert in these folds.

The preparation is rather macerated, and as tends to happen in this connection, the glandular epithelium of the folds in this part of the provagina has sloughed off, so as to expose the underlying musculomembranous supporting tissue. Some of the musculoid fibers inserting in the folds are visible through those membranes, as indicated by the fine, short, diagonal lines in the figure.

Outward strata of tissue of the provagina are chiefly composed of massed musculoid fibers arranged diagonally, semispirally, or more or less circularly. The retractor-depressor fibers of the folds issue from this tissue, which in effect makes up a long, cylindrical constrictor of the tract. The provaginal constrictive musculature is quite substantial, but this is not very evident in its less concentrated states. It has indefinite limits, merging gradually with the delicate musculoid tissue of the uterus as the latter gives way to the provagina. In the expanded anterior provaginal region it tends to split off from underlying tissues so as to form a sort of sleeve around the tract. In physiological salt solution the vagina shows occasional strong peristaltic contractions, during which its broadened anterior end contracts especially strongly. The uterus pulsates rather feebly in correlation with such contractions. These actions are due to intrinsic musculature, and occur after the organs are dissected free from all other structures. The uterovaginal region has extensive extrinsic musculature which must add considerably to its muscular capabilities. This musculature mostly consists of innumerable fine, short fibers partly organized into many small bundles and "slips." These small elements mostly originate from the floor of the lung (or "diaphragm," which itself is fairly muscular, though very thin) and from the part of the columellar muscle which underlies the uterovaginal region. Those elements arising from the columellar muscle are partly associated with the midbody septum (cf. Fig. 2) and they are partly formed into scattered, relatively coarse slips. They angle dorsad and shortly insert on the right lower side of the female tract, and at the elbow at the beginning of the provagina (while some adjacent similar elements insert on the prostate). The provagina is held to the lung floor along its length by great numbers of fibers standing up on its surface. When dissected free of the lung, that organ looks very fuzzy or hirsute because of such fibers distributed over its dorsal face. Much of the uterus is closely fixed to the lung floor by hardly detectable fibers. The various extrinsic fibers, as a whole, chiefly must function as dilators and suspensors of the female tract, with the aid of the lung, which can also compress the vagina.

With the obliteration of the rapheal column in the provaginal region, the roofing mechanism of the seminal gutter becomes clearly identifiable as a flap-like structure. This rapheal fold is quite narrow in this region, much less so than the figure seems to suggest. The gutter is also not very developed in the provagina, but it is clearly traceable into the outlet of the duct of the seminal receptacle. The duct of the receptacle is strongly, longitudinally plicate internally and the gutter arises from a cleft which separates 2 of the plicae in the duct. One or more prominent folds may issue from the duct into the vagina proper. These seem to be of no special nature, and are not consistently developed; however, they may function as penial guides in copulation. The basal portion of the receptacular duct actually functions as a vagina in conjunction with the vagina proper (cf. Fig. 91). The vagina proper consists of a quite narrow, tapered epithelial tube, and an encircling sphincter, which is formed of a dense concentration of semi-circular or semispiral muscle fibers. The sphincter sometimes seems to be incompletely divided into 2 successive muscular masses tightly appressed to each other. It usually has the bulbous appearance indicated, but is sometimes more elongate and fusiform, when the enclosed vaginal tube tends

to be kinked or S-shaped. The sphincter when preserved stands out from adjacent organs in being especially shiny-reflective and practically colorless (which is evidence of its muscular nature). The tapered end of the vagina proper, and part of the sphincter, is embedded in the body wall of the snail, nearly vertical to that wall. The vaginal tube is capable of protruding to a varying extent, but only slightly, on the external body surface, where it shows 2 ill-defined lips, which are usually very bright yellow. While the female pore is constantly tiny in the indicated typical condition, it must open in some individuals at times to the remarkable diameter of several millimeters to allow passage of egg masses of comparable width (cf. Fig. 51).

The main body of the uterus must be assumed to create the larger part of the thick, firm, lamellated gelatinous wall of the egg mass, and to shape it to the capsular matrix of the mass. The lamellated wall is not completely formed over the bottom or attachment surface of the mass, so that the matrix tends to be exposed along a "raphe" on that surface. The mass probably is formed by considerable pressure into a cross-sectional C-shape as it develops; in the process the longitudinal concavity is probably forcibly fitted down over the rapheal column of the uterine tract. Thereby, the column may block formation of the firm wall over the concave side of the mass, while preventing the capsular matrix or capsules from being forced out of the so-created gap on that side. The muscularity of the provagina doubtlessly is essential to giving the egg mass its definitive form and extruding it to the outside of the animal. The vaginal sphincter may aid in this, but it is essentially a copulatory structure (cf. Fig. 91). Since the uterovaginal division of the tract is at most about 15 mm long, and since egg masses may be almost twice that length (cf. Fig. 51), it seems evident that in oviposition the "anterior" end of the egg mass may issue from the female pore of the snail before the mass is completed at its trailing end. The outermost flaccid coat of the mass possibly is formed by the epithelium of the provagina. Lymnaeids reportedly use their mouth, but not their foot, in aiding the egg mass to attach itself to a substratum. The egg masses seem to be provided with a special substance which cements them to their attachments; such cement possibly is provided by the yellow V-folds (cf. Fig. 63) in the provagina.

FIGURE 67. The uterine cecum and uterine neck viewed from the non-rapheal side. The preparation is preserved, and is the one represented in Figs. 65 and 68. In the living state the appearance is smoother. Some of many numerous fine musculoid fibers which cross the surface of the neck transversely are suggested by fine lines. In the figured condition, the bulging folds at the base of the cecum are very well defined. They and the near side of the cecum are highly glandular and brittle in preservative. The dashed lines running along the neck indicate lines of invagination of glandular folds. Full views of the dissimilar opposite side of the cecum and neck are shown in Figs. 51 and 63.

FIGURE 68. The uterine cecum, in "top view" (cf. Fig. 65). The rapheal fold is formed by a very deep invagination of the wall. The left half of the organ perhaps functions in aligning egg capsules in the egg mass and the other half probably serves as a secondary seminal reservoir (cf. Fig. 65). The left half in life has a rather thick yellow-orange glandular wall. The wall of the right half is thin, almost membranous, only slightly glandular, and hardly yellowish. It has a pearly look from internal reflections; it does not become brittle from overpreservation, as does the other half. The organ figured here shows a narrowed shape which represents an approximate extreme (cf. Fig. 69); this probably has resulted

largely from contraction of circularly oriented musculoid fibers in its wall, but partly also from shrinkage due to preservation. The terminal hooking of its end is characteristic.

FIGURE 69. The uterine cecum, in the relatively relaxed state, viewed on the face opposite to that shown in Fig. 68, with a portion of the adjoining uterine neck. The neck has been cut transversely to reveal how its internal folds largely fill the lumen, and how they relate to the seminal gutter (cf. Fig. 65). At such a cut face the prominence of the gutter's ciliation is evident. Note that 2 folds combine to set off the gutter from the remainder of the lumen of the neck. The given example is unpreserved and relatively smooth. It is transversely expanded to its normal limit, and rather flat. This condition is probably due to the action of both intrinsic and extrinsic musculoid fibers, and to compression by adjacent organs. The face in view is shallowly concave, and it fits longitudinally and tightly over the end of the free uterine limb (cf. Figs. 57 and 74). Its shape, exactly as shown, is quite characteristic of the population represented. Note that the oviducal outlet faces into the rapheal side of the cecum.

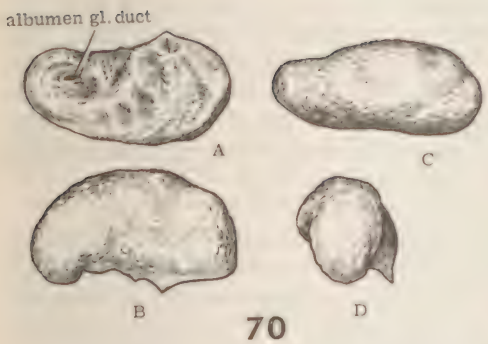
FIGURE 70. The albumen gland of an adult specimen as seen from several angles. A, the side which in the natural position is intimately appressed to the carrefour complex; B, the broadest, approximately ventral side; C, the side approximately opposite to that in A; and D, view of the smallest end. The side directly opposite to that shown in B is shown in Figs. 51 and 71. In A, the side shows elevations and depressions which represent a partial mold of the free uterine limb and a portion of the oviducal labyrinth. The normal adult gland is orange-pink to orange in color, but it varies toward a plain yellow. The orange color may be intense, and this perhaps reflects a transient state of peak physiological activity. The gland is finely textured over its entire surface by pustular to somewhat vermiform slight extensions of the fine tubules of which it consists. These mostly tend to form minute polygonal areas which are outlined with dusky pigment. Therefore, a faint, fine, reticulate pattern is formed over all the gland's surface. This pattern is the external indication of a complex of supporting tissues in the gland. The organ is relatively firm and densely glandular, and it may become quite hard in preservative.

FIGURE 71. The albumen gland of 3 adult specimens showing variations in form and size. They are drawn to the scale given in Fig. 75. The views are directly comparable to that in Fig. 51. The position of the duct of the gland is indicated toward the right end of each drawing. The size of the organ seems to be readily affected by factors relating to nutrition, infections, aging and physiological cycles. In its ontogeny, when the gland becomes an evident entity, it is relatively elongate and shaped much like the example on the left, which is pale in color and juvenile in appearance, despite the fact that the specimen it came from falls within the adult range in shell-length (note the figure in parentheses). That specimen was judged to have never overwintered, and was collected in the late fall. Conchologically and anatomically it appeared to be an unusually robust adolescent or subadult individual. It appeared that the albumen gland had been unable to keep up with the other organs in growth. The second example from the left is an unusual variant in being relatively short. Despite the very large size of the specimen it represents, it is rather small, but it was normal in texture and color. It possibly had previously acquired a larger size, and perhaps had increased and diminished in size several times in its history in relation to reproductive cycles.

Maybe its small size is a reflection of recent oviposition by the specimen. The gland must give up much of its volume in that process (cf. Fig. 57). The largest example shown was markedly larger than any other seen; in specimens of equal size, and up to 5 mm longer, the gland was usually nearly 2 mm shorter. The size of the gland of other snails not rarely was markedly above the average, and it is suspected that this is a transient condition which shortly precedes oviposition. The gland may retrogress greatly in size and become dark and brown in specimens thought to be stunted or especially senile. The same effect clearly relates to trematode infections. However, the organ remains robust and normal in color in very large adults which appear to be healthy.

FIGURE 72. The albumen gland, cut open longitudinally, A, and shown in transverse section, B, to reveal its gross internal structure. The drawings are somewhat generalized, in respect to some features about which there is uncertainty. The organ consists of hundreds of densely massed, vermiform, glandular tubules, each of which has a nearly closed filiform lumen that runs its length. Such lumina are exaggerated in the figure. The tubules are mostly very long, and appear to be grouped into at least a dozen blocs, which are intergrown with each other. The tubules of each bloc seem to be the branches of one or a few tubules identical to them in appearance, which terminate with others in one of a number of trough-like extensions of a longitudinal central cavity. The cavity is S-shaped in cross section, and each arm of the "S" gives rise to a series of troughs arranged in a somewhat radiating pattern. Each bloc of tubules follows a curving course extending away from the central cavity, so that most tubules meet the surface of the gland at a curved angle, and so that some tend to run along that surface for a short distance (cf. Fig. 74). The blocs partly tend to wrap around the central cavity and bulge into it. The relationship of the lumina of the tubules and of the albumen gland duct to the central cavity was incompletely worked out. The central cavity does not seem to lie entirely within epithelial walls. A thickly membranous, epithelial stratum clearly bounds one side (the upper side of the "S" in the figure) of the cavity, where it is rather loosely attached in part; that stratum is continuous with the wall of the albumen gland duct of which the portion lying within the gland seems to be free of the adjacent tissue. A prominent artery enters the gland alongside the duct. Inside the substance of the gland there is a complex of arteries, involved with a substantial skeleton of membranous and fibrous musculoid elements which ramifies throughout the organ. Parts of this framework of tissues extends from the gland's broad ventral side, and are joined to an irregular loose web of arterial vessels and fine fibers which lies over the dorsal surface of the gizzard and extends onto the nearby portion of the postintestine (cf. Figs. 2 and 48). The full length of the duct of the gland is shown in A. The duct has a number of longitudinal plicae (not shown; cf. Fig. 57) which pass to the edges of the lips, at its outlet, where they are quite large.

FIGURE 73. The nidamental gland (or matrix-gland) of an adult specimen in 2 different views. The top drawing shows the face which is appressed to the terminal end of the free oviducal limb, and to the uterine cecum, in the natural position (cf. Figs. 57 and 60). This face is toward the top in the lower drawing. The form indicated is definitive, but it is distorted transiently during its functional activities. It has a complex surface pattern formed by the dusky lines of invagination (cf. Fig. 74) of a membrane which forms the outer wall of the organ. Note that the lines of invagination meet or split in many places, or give off series of other lines. The entire gland stalk is shown; in this example it was attached



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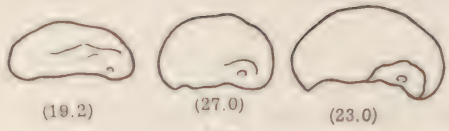

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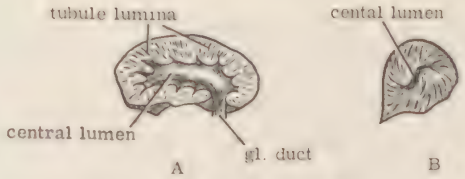

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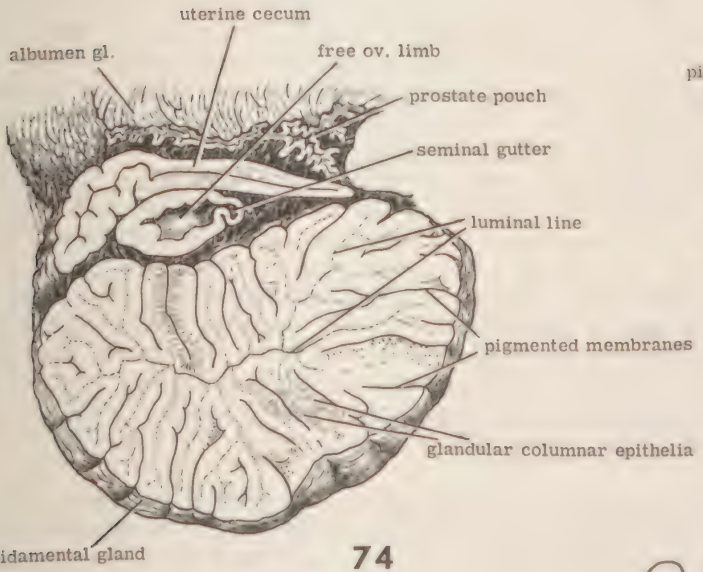

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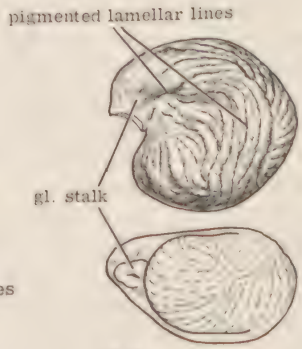

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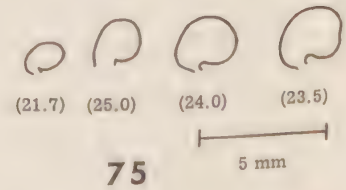

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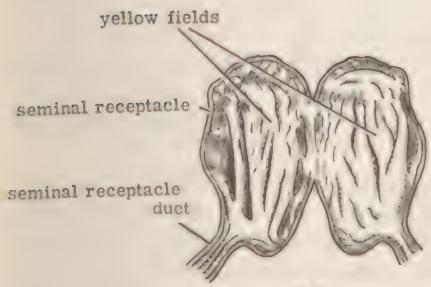

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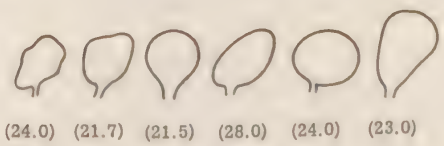

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broadly to the female tract. The organ tends to curl part of the way around the tract, in the natural position. It is translucent, greyed by dusky pigment, and yellowish; it is sometimes rather intensely yellow, but it is always of a duller, more greenish cast than the uterus. In preserved specimens it may look as if it were inseparable as an entity from the uterine cecum, but the latter is commonly less dusky. The gland probably secretes the voluminous matrix in which egg capsules are embedded in the egg mass (cf. Figs. 51 and 57).

FIGURE 74. The nidamental gland, and organs that are adjacent to it in nature, cut cross-sectionally so as to reveal their gross internal structure and positional relationships (cf. Figs. 57, 58, 60, 69 and 72). The nidamental gland, the free arm of the oviduct, and the uterine cecum, are cut transversely near where they unite with each other. The organs are held together by a complex of partly muscular fibers and fine arterial vessels which evidently put constant pressure on the several organs, and thereby tend to force the secretion of the nidamental gland out of its stalk. The external membranous wall of the gland, which is partly formed from a fine network of muscle strands, tends to do the same. The gland is capable of contractile pulsations. The pigmented membranes are double walled invaginations of the outer membrane of the organ and they form the internal supports of large glandular lamellae. The pigmentation is associated with a fine arterial network ramifying in the spaces between the walls of the membranes. Note how the membranes bifurcate or fuse in various places (cf. Fig. 73). Some are curled along their length, and tend to be semi-tubular. Each wall of each membrane supports a thick layer of quite large high-columnar epithelial gland cells having basal nuclei. The cells are visible at the given magnification, as indicated by fine lines vertical to several of the shown membranes. The luminal ends of the gland cells evidently disintegrate readily, and this results in partial fusion between lamellae that come into contact with each other. In cross-sections, the lumen is then detectable only as an interrupted vague branching line. This seems to be an almost constant condition in the gland. The lamellae of the uterus are quite like those of the nidamental gland in structure (cf. Fig. 66).

FIGURE 75. The nidamental gland of 4 specimens, showing variations in form and dimensions. It is one of the most variable of the organs in respect to its size, which differs from specimen to specimen. The indicated variation probably depends largely on functional states, but also partly on the degree of contraction or swelling it undergoes in preservative. The organ swells in water, or when underpreserved, and it shri· ks when overpreserved, especially in alcohol. These effects may be quite extreme. The organ must give up much of its substance during egg-mass formation, and it probably remains in a shrunken state for a succeeding period of time. The thickness of the stalk (cf. Fig. 73) varies considerably, doubtlessly in relation to function, while the size of the oviducal outlet (cf. Fig. 65) varies directly with the thickness of the stalk. The stalk always is short, and in all the examples shown it was severed exactly at its terminus.

FIGURE 76. The seminal receptacle of a living specimen, showing its changes in shape during pulsatory activity as seen in physiological salt solution after being separated from its attachment to the pericardium (cf. Fig. 2). It is filled with the usual material (cf. Fig. 78) which must exert an outward pressure on its walls. The organ contracts and expands rhythmically, changing several times in several seconds from one to the other of the shapes figured. The change largely results from powerful contractions of the basal part of the organ surrounding its outlet

into the receptacular duct. This action usually is not very obvious when the organ is in its natural position, but it apparently tends to occur continually, without direct relation to mating. Freeing the organ from its attachment seems to stimulate it to increase its muscular activity. Mechanical stimulation of its base sets off a strong peristaltic wave which travels about halfway down the receptacular duct. When the organ is detached from the pericardium, its duct becomes very much shortened, thick, and notably constricted at its receptacular juncture. Internally, the duct has 2 or 3 large longitudinal plicae and a few smaller ones, which run its length (cf. Figs. 66 and 78). These plicae appear to have rather strong musculature, seemingly of mostly longitudinal fibers, but partly of evident diagonal fibers. Circular fibers surround the duct along its length; they are prominent at the duct's juncture with the receptacle and they are highly developed in the basal part of the duct, where they merge with the muscle strata of the vagina proper. Some musculoid fibers fan out from the duct, meridionally onto the outer wall of the receptacle. In its natural position, the organ is sandwiched between the pericardium and the lung, where it is partly embedded in a mass of arteries and criss-crossing musculoid fibers which attach it to those structures. These various elements must put pressure on the organ and tend to flatten it. Cilia were not detected with certainty in the receptacle or its duct; however, a channel is formed between 2 of the duct's plicae, which resembles the seminal gutter of the main female tract. The function of the receptacle as a seminal reservoir in basommatophorans, has been doubted, as authors rarely have found quantities of normal-seeming sperm in it (cf. Fig. 78). It does serve as a bursa copulatrix (cf. Fig. 91).

FIGURE 77. The seminal receptacle of 6 adults, preserved and "fresh," illustrating its intrinsic form and size and related variation. They are drawn to the scale given in Fig. 75. The 2 examples furthest to the left, and the largest, are relatively empty and are more or less flatly collapsed, as is seen in some adults in various seasons and in most juveniles. The other examples are filled out spheroidally by internal contents. The organ is highly distensible, and it is believed that large quantities of sperm are delivered to it in mating. It probably varies greatly in size in relation to reproductive activity. The apparent variation in the figured organs is exaggerated by differences in orientation of the different examples. They are almost completely bilaterally symmetrical. In a side view, as given in all but one of the figures, they are more or less asymmetrical in outline, but when viewed from the end as in the third example from the left, they look symmetrical. The form is altered by inflation, to a degree that depends on the volume of the contents. Even the most angular and elongate organ evidently takes on an almost perfectly globular form when expanded to the extreme. Globular, yet larger examples than any of those figured were seen. Ontogenetic observations indicate that there is considerable truly individualistic variation in the intrinsic shape of the seminal receptacle. Distinctive differences in shape are clearly revealed only when the organ is collapsed. Organs in that condition were repeatedly seen to be rather "hatchet-shaped," in near-correspondence to the form of the example on the far left. In ontogeny the organ develops in the flattened state, in that hatchet-shaped form, which becomes established when the snail reaches a length of about 8 mm. The organ takes on a yellowish color when the snail grows about a millimeter longer. In some snails having a shell-length between 10 and 13 mm (first-year, not overwintered snails) the organ exhibited brilliant yellow elevations on its walls (cf. Fig. 78). The receptacle of these snails usually contained a mass having the same appearance and color as

that generally found in the adult organ. It seems then that at least sometimes snails mated as acting females in their first growing season well before they reached fully adult size. It was not confirmed, but it is suspected that it may have been the rule in the population for the snails to mate as females in the pre-adult state, and that most near-adult snails carry a receptacular store of spermatic substance when entering into their first winter.

FIGURE 78. The seminal receptacle of a large adult, in the collapsed state, cut open longitudinally and folded open to show its inner walls. It is the same example as shown on the far left in Fig. 77. In the collapsed state features of the organ which are very obscure in the inflated condition are evident. The elevations visible on the wall are formed from a tissue which is brilliant yellow in life, and the outlet of the organ is largely surrounded by a semispiral ridge or lip of such tissue. The elevations are branched or split glandular thickenings of the wall and are not folds, although there are several slight invaginations of the organ's wall associated with them. They are largely fused with each other and form 2 glandular fields in the organ. These fields evidently are less elastic than the remainder of the organ. When the organ is inflated the fields split and fan out in a branching semi-meridional pattern from the base of the organ. They are less stretched in the basal area and tend to remain in evidence there; on the wall opposite to that, they then are stretched very thinly and are hardly detectable. It appears that the tissue between the main thickenings then becomes exceedingly finely dissected by development of numerous close-set short splits. This seems to be indicated by a very fine, whitish, latticed or scaly pattern, which shows through the wall of the organ. The apparent splits are mostly developed parallel to each other within a broad diffuse zone which tends to encircle the organ roughly subequatorially.

Large whitish masses of sperm were rarely found in the seminal receptacle, except in snails (acting females) whose mating had been interrupted just before being preserved or dissected. The contents of the well-expanded organ in hundreds of routinely collected specimens consisted of a partly viscous and partly solid multicolored mixture of several substances containing some whitish material which look like massed sperm. Often there was a tan or red-brown, diffuse, semifluid material concentrated in an ovate "polar" area against the receptacular wall and opposite to the outlet of the organ. A translucent, semisolid substance commonly covered most of the remainder of the wall. This clear material usually enclosed a mass which almost always had largely a pale or intense pink color, but which often contained a white mass ropy-fibrous in texture, or white clumps of cheezy consistency. These various ingredients tended to be "swirled" together in a way that suggested that the mass had undergone rotation on an axis in line with the brownish "polar cap." The mass commonly also contained yellow cheezy lumps, chunks of an intense orange material, and crystalloid granules which were bright yellow-orange to rusty brown. At the approximate center of the mass a deep red chunk of variable size often occurred. In external view the filled seminal receptacle most commonly looked predominantly purplish- or violet-pink. The organ was never seen to be a deep uniform orange-yellow as is constantly seen in some species of lymnaeids. The crystalloid granules looked quite like those which regularly occur in the ovotestis (cf. Fig. 53). Many of these clung to the yellow elevations of the receptacular wall as do the granules in the yellow oviferous zone in the ovotestis. Perhaps the granules partly come directly from another snail in mating.

The preceding observations suggest that sperm go through an elaborate

"processing" in the seminal receptacle, in which perhaps large quantities of them that may be superfluous to later stages of the insemination process are destroyed. The yellow tissue of the receptacular wall may have a sperm "ingestion" function. As the narrowness of the seminal gutter (Fig. 66) suggests, only small quantities of "ripened" sperm may ever pass from the receptacle, perhaps in tiny packets. The contents of the receptacle then may be mainly breakdown products of spermatic matter. They perhaps are also partly products of the breakdown of ova, nurse cells, and even egg capsules, introduced by an acting male snail into the receptacle (cf. Figs. 57 and 62) or acquired from the adjacent female tract as debris of egg mass formation. In 2 specimens, albuminoid bodies which almost certainly were incompleted egg capsules, coated by a thin membrane and containing an ovum, were found in small numbers on routine examination of their receptacular contents.

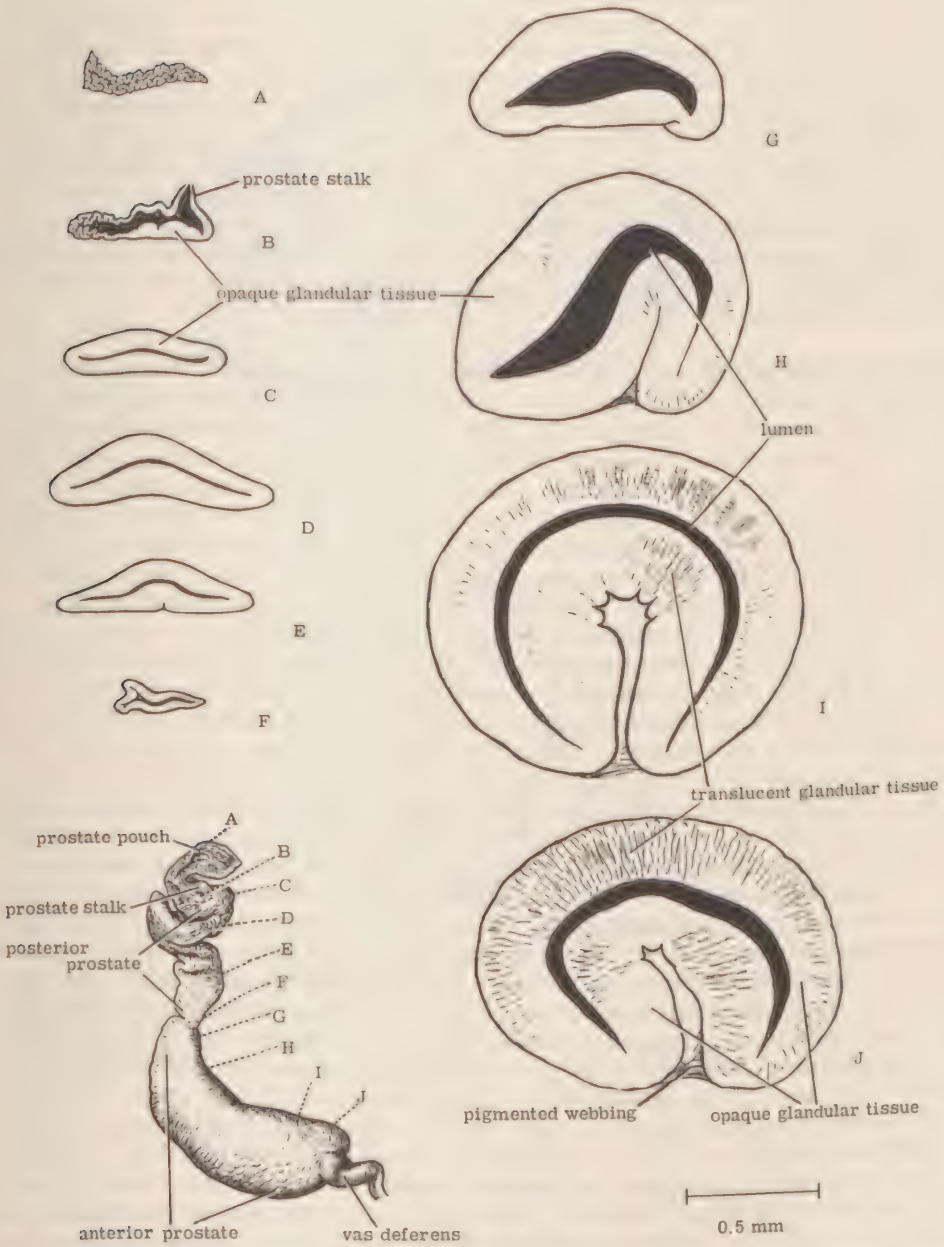
Evidence that a mating season may closely precede or largely coincide with a highly restricted egg-laying season (Figs. 1 and 56) might suggest that ripening of sperm in the seminal receptacle could be a brief process, or might not really occur. On the other hand, it may be that receptacular storage and ripening of sperm are long-term phenomena. It appears that the snails may commonly mate as acting females as pre-adults, and overwinter with a receptacular store of spermatic material (cf. Fig. 77) prior to their first egg-laying season, and that they thereafter generally maintain such a store throughout the year. This indicates that mating may occur not infrequently in different seasons, and that the breeding period in the spring represents only a great peak of intensified and exhaustive mating activity. Such a peak could be only coincidental to oviposition activity in the same season, and might serve to store sperm destined for fertilization in the next year's ovipositing season. A seasonal relationship between breeding activity and the volume and character of the contents of the organ was not discovered.

FIGURE 79. The prostatic tract in ventral view and sections of the same made at levels indicated by the given letters, with a portion of the succeeding tract in place. The sections represent thick slices viewed by intense reflected light. Section B is somewhat diagrammatic, while the other sections are shown exactly as seen in the particular specimen. The generally dorsal side is shown turned downward in the sections. The natural position of the prostatic structures is indicated in Figs. 2, 51, 58 and 60. The form of the parts is highly constant. The stalk and the posterior and anterior prostates are distinguished on a topographic basis; they appear to be essentially alike in their nature. All parts but the pouch are more or less yellow-orange in life. The posterior prostate is rather ribbonlike throughout, but in its natural position it is so twisted and folded upon itself in its posterior part that it appears to be more massive than it is. However, its curving transverse course from level C to the right (to the left in the drawing), which ends at a pronounced elbow, as indicated, is a constant feature. The figure represents the natural pose, but in a somewhat contracted specimen; in fully extended snails the posterior prostate is straightened out so as to be longer and narrower than it looks here, and the indicated transverse folding at the level just posterior to section E is not present.

The prostatic tract begins as a flat, triangular stalk which arises at the juncture of the hermaphroditic duct and the insemination pocket (Fig. 62). The stalk gives rise to the posterior prostate just as the latter gives off the prostate pouch as a lateral diverticulum. The pouch is very thin-walled, and almost always has been found to be flattened, empty, and highly wrinkled. It tends to be duskily

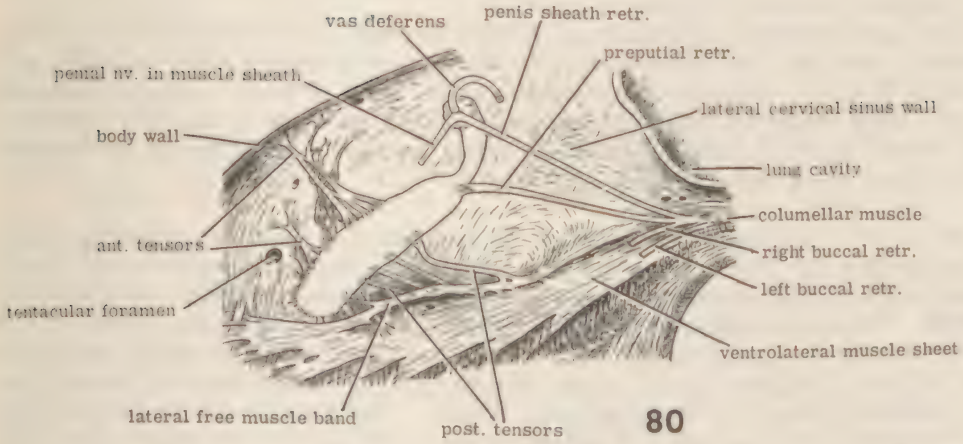
pigmented and is often blackish. By means of a longitudinal slit (which is open in section B) having a lip-fold formed along one side, the stalk opens into the passageway between the pouch and the posterior prostate. Thick prostatic tissue of the latter extends into the base of the pouch so as to block the passageway to a large extent. The arrangement is such that a slight compression of the tract at that level would block the entrance into the posterior prostate and force any material coming from the stalk to enter the pouch. The pouch is highly constant in shape and texture. When empty it is sharply flexed near its base, and in its natural position it appears to arise at a sharp initial flexure of the prostate. Its lumen was found to be longitudinally divided by a delicate membrane in one specimen, but whether this condition is constant is unknown. The function of the pouch is conjectural. It apparently does not store sperm. On occasion it has been found to be somewhat swollen by a clear to slightly milky fluid, including once when the stalk was found gaping widely into the insemination pocket and the hermaphroditic duct. The clear fluid possibly becomes a part of the semen during mating. In 2 snails which were preserved just after interrupting their mating as acting males, the pouch was found to be enormously distended by a very dense and firm mass of sperm. In one of these specimens the sperm mass extended broadly and deeply into the prostatic tract, all the way into the anterior prostate, and the pouch was almost unrecognizable because its walls were stretched so thinly as to be almost undetectable, and because its outlet was enormously stretched open. The posterior prostate then was found to be forced into a cylindrical shape, and its wall was stretched very thinly. Also, the constriction demarcating the anterior and posterior prostates then was obliterated fully by stretching of the walls. In a specimen of another form of *Lymnaea catascopium* (*"reflexa"* Say), the anterior prostate was found so filled with sperm that its single fold had been forced outward and totally obliterated; its wall in cross-section was then entirely circular.

The substance of the prostatic tract, on the whole, is of a firm, cheezy-glandular, fibrous nature, and cut surfaces largely have an opaque featureless appearance (indicated by the clear areas in the figure). In the more anterior portion of the anterior prostate, diffusely defined irregular areas often tend to be translucent. In preservative, these areas become hard and brittle, while the opaque substance tends to remain "cheezy." The outer prostatic wall is greyed by pigment which forms a reticulum of dusky tracings outlining a mosaic of minute, partly elongate, polygonal areas. The polygonal areas project as slight pustules. The tract is enclosed in a delicate meshwork of musculoid fibers which tends to form a membranous surface stratum. Evidently this is invaginated deeply so as to form tubular sheaths of fascicles of elongate gland cells. Evidently each polygonal area on the outer prostatic surface represents the end of such a fascicle. In the more translucent areas, as indicated in sections I and J, fine, densely packed, seemingly columnar and fibrous elements vaguely can be seen aligned vertical to the inner and outer surfaces of the tract. These seem to represent fascicles of cells and their sheaths. The observed fine striae transverse to these, as shown, may represent circularly arrayed fibers passing among the fascicles. A substantial skeleton of supporting tissues ramifies among the prostatic tissues, but this is not apparent in examples not specially treated. Appearances suggest that the prostatic wall is structured similarly to the main tissues of the albumen gland (cf. Fig. 72). It may doubtfully be suggested that it is composed of fine modified tubules. The prostatic wall facing the lumen everywhere looks smooth and featureless, except that on close inspection one seems to see exceedingly fine, well-spaced pores generally dotting it. Cilia were not definitely detected in the prostatic tract; if present, they must be very fine or sparse.

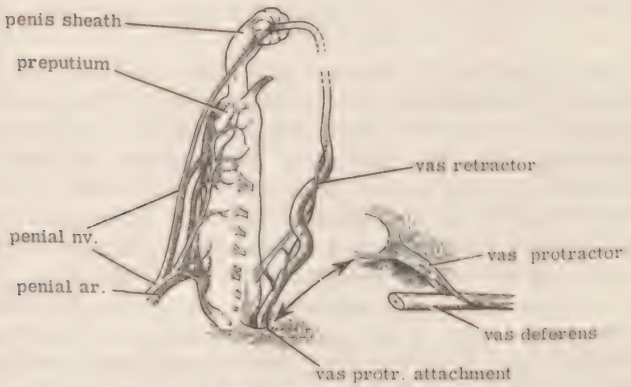

A
prostate stalk
B
opaque glandular tissue
C
D
E
F
G
H
lumen
I
translucent glandular tissue
prostate pouch
prostate stalk
posterior prostate
anterior prostate
vas deferens
J
pigmented webbing
opaque glandular tissue
0.5 mm

Note that a weak fold tends to run the length of the posterior prostate, in line with the prominent fold in the anterior prostate. The way in which the 2 prostates are set off by a constriction is constant. The posterior angulation of the anterior prostate, to the left in the drawing of the whole tract, is characteristic of the snails studied, and the prostatic lumen extends into it. On the dorsal side of the anterior prostate a transverse linear depression is formed across the right longitudinal swelling next to the line of invagination of the fold (cf. Fig. 51). A substantial artery lies in this depression. Another substantial artery is transversely impressed into the dorsal side of the tract exactly where the posterior and anterior prostates are demarcated from each other. When the anterior prostate is not "overpreserved" the sides of its fold can be pulled outward and completely flattened. The 2 sides are only loosely bound together by a webbing of partly musculoid fibers.

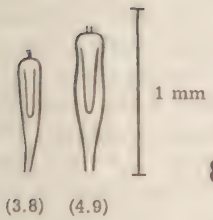
FIGURE 80. The penial complex in its natural position in the cephalopedal hemocoel, and its extrinsic musculature. The preputial retractor is fused with the right buccal retractor, at its origin. The penis sheath retractor is fused at the head of the sheath, with a sleeve of muscle which encloses a branch of the penial nerve (cf. Fig. 81). The tensors represent the "preputial protractors" of the literature. They must serve as retractors of the preputium, at least incidentally, while primarily they probably function in holding the basal half of that organ in its figured position during initial stages of eversion (cf. Fig. 86) of the penial complex, when the upper preputial end inverts by slipping inside itself (cf. Figs. 84, A, B, D, and 87, B, C). Pressure of blood in the cephalopedal hemocoel may aid in this initial stage, but eversion probably is initiated by prolongation of the penis sheath. If at that time the sheath retractor and the muscle sheath of the penial nerve contracted, they might tense the upper end of the sheath, "anchoring it in suspension," and if the preputial retractor also relaxed then, the lower end of the sheath on elongating would begin to force its way into the preputium (note in Fig. 84, A, how the lower end of the sheath may elongate). This would cause the preputium to begin to slip into itself. Contraction of the muscle sheath of the penial nerve might actually force the penis sheath part of the way into the preputium. Possibly, as soon as partial inversion of the preputium is accomplished, the inverted part may literally crawl, wormlike, toward the preputial base, gaining purchase on the part of the preputial wall then fitting closely around it. When the organ is inverted to the level of the preputial tensors, and if the latter relaxed in the appropriate sequence, pressure of the surrounding hemocoelic blood could come into play as a force which alone might rapidly complete the inversion process. However, the first indication of the extrusion of the penial complex to be seen on the outside of the animal is an eversional, rapid "blossoming out" of the preputial base through the male pore. This probably occurs after the upper end of the preputium has become inverted for some distance. It probably results from the combined actions of relaxation of the more basal tensors, contraction of "somewhat circular" muscles in the adjacent portion of the preputium (cf. Fig. 85, O), contraction of the 2 major longitudinal muscle tracts in the preputial wall (cf. Fig. 86, B), and of pressure of blood in the cephalopedal hemocoel. The more or less circular preputial muscles largely enclose the other preputial tissues as a partially loose sleeve. Their contraction might tend to squeeze the other tissues out of the male pore. Concurrent contractual shortening of the longitudinal preputial muscle tracts would pull the preputial walls toward the male pore, enhancing the extrusive pressure. The latter tracts originate partly by radial fibers in the body wall at the male pore (cf. Fig. 49); on contrac-


vas deferens
penis sheath retr.
preputial retr.
penial nv. in muscle sheath
lateral cervical sinus wall
body wall
lung cavity
columellar muscle
ant. tensors
right buccal retr.
left buccal retr.
tentacular foramen
ventrolateral muscle sheet
lateral free muscle band
post. tensors

80


penis sheath
preputium
vas retractor
penial nv.
penial ar.
vas protractor
vas deferens
vas protr. attachment

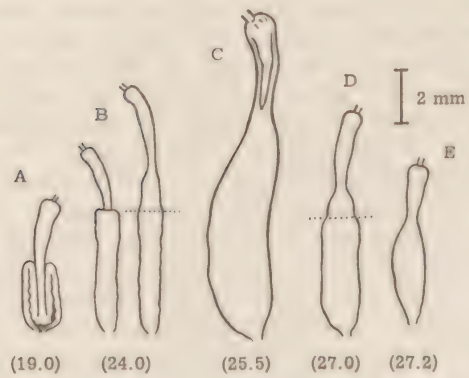
81


1 mm
(3.8)
(4.9)

82

1 mm
(9.3)

83


A
B
C
D
E
2 mm
(19.0)
(24.0)
(25.5)
(27.0)
(27.2)

84

tion, the radial fibers might pull the sides of any partly extruded portion outward, peripherally from the pore. At this stage blood pressure probably takes over as the primary force in completing eversion.

The tensors insert along the edge of the 2 primary folds ("pillars") of the preputium. Note that the posterior tensors insert on a loose band of muscle that is split off from the ventrolateral muscle sheet. Most of them insert on the band's lateral side, which is hidden in the given view. The muscle sleeve or sheath of the penial nerve is often very coarse, but it varies considerably in development from specimen to specimen (cf. Fig. 81).

FIGURE 81. Extrinsic musculature of the vas deferens, along with the penial complex and its primary nerves and arteries. Also shown are cut ends of the posterior preputial tensors aligned along the posterior primary fold of the preputium. The penial nerve arises from the right cerebral ganglion and the penial artery arises in close contact with it (cf. Figs. 30 and 32). At their origin they are enclosed together in a coarse sheath of longitudinal muscle arising from membranous tissue on the ganglionic collar. The muscle sheath is eliminated in the figure (cf. Fig. 80). It passes to the depression on the head of the penis sheath, where it inserts, partly on the vas deferens. It is split open in its lower course; through the slit formed thereby, relatively thick and short main branches of the nerve and artery pass out of it to the preputium, but before they do, they both send off a delicate long branch to the head of the penis sheath within the sleeve.

The vas deferens has 2 primary divisions (cf. Fig. 85). One division lies in the body wall in a canal which fits closely around it for much of its length, and it can slide freely (at least in part) along that canal. The vas protractor functionally originates on the dorsoposterior edge of the anterior U-shaped opening of that canal as a very thin muscular band, which forms the anterior part of that protractor. This band is an anteriorly directed extension of a delicate musculomembranous sleeve that encloses much of the portion of the vas that lies in the body wall, and that forms the remainder of the protractor. The sleeve arises by separating off from a layer of longitudinal muscle which forms the external tissue layer of most of the vas. It is partly composed of 2 longitudinal bands, lying on opposite sides of the vas, and of crisscrossing muscle fibers. The side of the sleeve under the vas is longitudinally split for some distance; the split widens as it runs in the anterior direction, so that the sleeve becomes converted to the anterior band on the dorsal side of the vas. The band's contraction would slide the vas forward and extend it out of the anterior opening of the canal in the body wall. The base of the preputium forms a wall on the anterior edge of that opening. When the penial complex is retracted, the vas extends from that opening into the cephalopedal hemocoel, wherein it loops widely and then attaches to the penis sheath. This free looped portion makes up the second division of the vas (most of the looped part is eliminated in the figure). The first portion of this division is attached to the preputial base by a set of several interconnected filiform muscle strands. One of these strands is practically an intrinsic muscle of the vas. This strand originates and inserts on the vas, at 2 widely separated points, and it courses along the vas between those points, spiraling about it as it does so. The several strands which make up the vas retractor are rather delicate and inconspicuous in many specimens, but rather coarse in others. The exact arrangement of the parts of the retractor varies from specimen to specimen. On contraction, the spiral strand would cause the portion of the vas which it spans to form a spiral loop. It would at the same time pull the portions of the vas lying between it and

the penis sheath in a direction away from that sheath, while contraction of the other parts of the retractor would do the same.

When the penial complex is fully everted and extended the anterior looped division of the vas is drawn entirely (or nearly so) into the preputium. When so everted, the preputium is practically vermiform and about 15 mm long (note that the looped division of the vas is about that long; cf. Fig. 85). Then, the looped division largely must be straightened out, and when copulation is in progress the penis sheath is shortened (cf. Fig. 91) so as to straighten it further. When the vas is drawn into the preputium, its retractor must be drawn into the same organ for its full length. Through the wall of the everted preputium of a mating snail, one can see the vas undergoing a rather violent movement, whipping from side to side. This action could be caused by rapidly alternating contractions of the vas retractor and protractor, and by correlated protractive and retractive contractions of the circular and longitudinal muscles of the vas. The action would also depend on the vas being anchored at the head of the penis sheath. If the vas retractor relaxed, and if a portion of the vas was protracted from the body wall, this could push the vas toward the penis sheath where it would be forced to bend to the side. This movement, repeated between retractive actions, would result in the whipping action. The vas in the body wall must see-saw back and forth within its canal during this activity, and the anchorage of the vas on the prostate posterior to it must affect that movement. The large permanent bend in the vas near its origin on the prostate may contribute a retractive force in this action by its passive elasticity. The general intrinsic elasticity of the vas could also contribute to retraction. When the protractor contracts, it probably stretches a portion of the vas just posterior to the insertion of its sleeve on the vas, and that portion would spring rearward when the tension on it was released. In one specimen the vas was found greatly retracted into the canal in the body wall, into which a large part of the anterior division of the vas was drawn; the vas of the body wall was largely coiled up near the female pore where it lay in the lateral cervical sinus (cf. Fig. 49). It may have burst into the sinus during a violent contraction of the animal, or perhaps a congenital anomaly was involved, but how it became so greatly retracted is not understood.

FIGURE 82. The penial complex of 2 juvenile specimens, showing ontogenetic stages (cf. Fig. 51). The complex becomes identifiable in the snail by dissection as an opaque white structure when the shell reaches the approximate length indicated on the left. The anterior division of the vas is traceable then as a delicate thread about as long as the complex, and it forms a tight loop extending from the apex to the base of the complex where it seems to attach and disappear. The preputium and the penis sheath then (cf. Fig. 81) are not separate entites. Later developments indicate that at this time, the incipient penis sheath is hardly existent and that the penis is almost entirely sheathed by the preputium. The head of the penis sheath differentiates morphologically from the preputium when the snail reaches the size approximate to that indicated on the right. Afterward, the remainder of the sheath differentiates and grows outward from the preputium as the penial complex grows rapidly in diameter in the region of the incipient velum and sarcobellum (cf. Fig. 87). The widening is largely due to thickening of the walls of the complex. The sheath grows more rapidly in length than the penis and begins to withdraw the penis from the preputium in the process. The sheath and preputium become well-differentiated when the snail grows to about 8 mm long, when the penis still extends for about a third of its length into the preputium. The sheath and penis then begin to take on their curved symmetry, the basal chambers

in the head of the sheath begin to become evident, and the penis shows an identifiable knot (cf. Fig. 83).

FIGURE 83. The penial complex in the subadult ontogenetic stage (cf. Figs. 82 and 84). At this stage the penis has not yet been fully withdrawn from the preputium by growth of the penis sheath. Because up to this stage the penis has grown more rapidly in diameter than the sheath, it fits tightly within the sheath. As a result, the penial knot is compressed and obscured; also, because the sheath is relatively narrow and thick-walled in its lower part, it constricts the penis subterminally, so as to leave the penial tip relatively expanded. The penis becomes fully withdrawn from the preputium by growth in length of the sheath when the snail reaches about 10 mm in length, and by then it has begun to lag behind the sheath in the increase of its diameter. The preputium is very tapered toward its attachment at the male pore up to this stage from having lagged in growth of its diameter in its lower region. When the snail grows to about 11 mm long, however, this region becomes expanded to a diameter equal to, or somewhat exceeding, the upper region, while remaining narrowly constricted at the pore. At the latter stage the penial complex takes on its essentially adult characters in proportions of its parts, texture, and color.

FIGURE 84. The penial complex of 5 adult specimens, showing variations in form, posture, and size relating to various factors. Examples A, B, and D are organs dissected from preserved specimens which had been "narcotized"; they were found to be in postures representing stages of the process of the eversion (cf. Fig. 80). Narcotization regularly seems to result in unpredictable degrees of contraction of parts of the complex, and often in its partial eversion. Example C is from a drowned specimen, and E represents a live specimen. In examples B and D the upper part of the preputium was found inverted into the adjacent lower part from the level indicated by the dotted line, and in dissection it has been forcibly pulled out of the other part. In example A, the preputium is shown in longitudinal section, so as to reveal how the lower end of the penis sheath is prolonged, and how the inverted part of the preputium is thrown up into annular folds which fit closely against the walls of the uninverted part. The latter condition suggests that the inverted part in life could creep, wormlike, toward the male pore. Example B shows a narrowed condition which apparently resulted partly from shrinkage in preservative, and partly from contraction of its complex musculature. This and the other 2 preserved examples even seem to have been reduced in overall size by effects of preservation, and in them the intrinsic form of the preputium is obscured. The specimen represented by example C was drowned to acquire a penial complex that was as relaxed as possible. Although it was not the largest snail dissected, its penial complex was of considerably greater dimensions than any ever seen. Its exceptional size apparently is partly due to unusually complete relaxation of its musculature. It exhibits what is taken to be the undistorted intrinsic form and relative proportions of parts that characterizes the population it represents. The convex outline on the left side of the drawing represents the anterior border of the preputium. Apparently, when the organ is retracted and in the living state, its musculature is always somewhat tensed, causing compression of its tissues and reduction of its volume. The shape of the penis sheath in the 3 preserved examples tends to conform to that of the enclosed penis because of contraction of circular muscles. Example E appears to be of somewhat juvenile character in the form of its preputium, as well as in size. Perhaps it represents a particular contracted condition, but in view of the extremely large size of the

snail it came from, it might be supposed that it has undergone atrophy or retrogressive growth. Further evidence of reduction of the size of the penial complex in relation to aging, as the figure seems to suggest, was not obtained. However, that the preputium has the capability of altering its volume and form greatly and to innumerable degrees is shown by its very great volume and length, and markedly different shape when it is fully everted and extended in mating. When everted and extended to the extreme, the preputium of a large specimen is about 15 mm long and about 3 mm wide at its base, where it is then considerably flattened horizontally. It is then circular in its distal more or less half, and regularly, smoothly tapered toward its free end, where it is sharply truncate (cf. Fig. 91). Its volume is then largely made up of venous blood and it gapes widely at its base into the cephalopedal hemocoel.

In the retracted state in life the preputium is light buff or tan in color, and rather yellow basally. The velar-sarcobellar structure is bright yellow and this color shows through the outer wall of the penial complex. The penis sheath is a cream yellow color generally, and fairly bright yellow in its lower part; it is rather translucent in its upper half, while the basal gland chambers are an intense lemon yellow. Dusky flecks are concentrated to form a dusky broad ring on the lower end of the penis sheath, except in specimens generally lacking dark pigment. Dusky flecking occurs in and on the walls of the penial complex, but it is notably sparse, even in heavily pigmented snails, and does not subdue very noticeably the intrinsic colors of the tissues. A densely white ring caused by a concentration of "calciferous concretions" occurs around the upper end of the preputium just where it joins the penis sheath, and where it is contiguous to the dusky ring on the sheath.

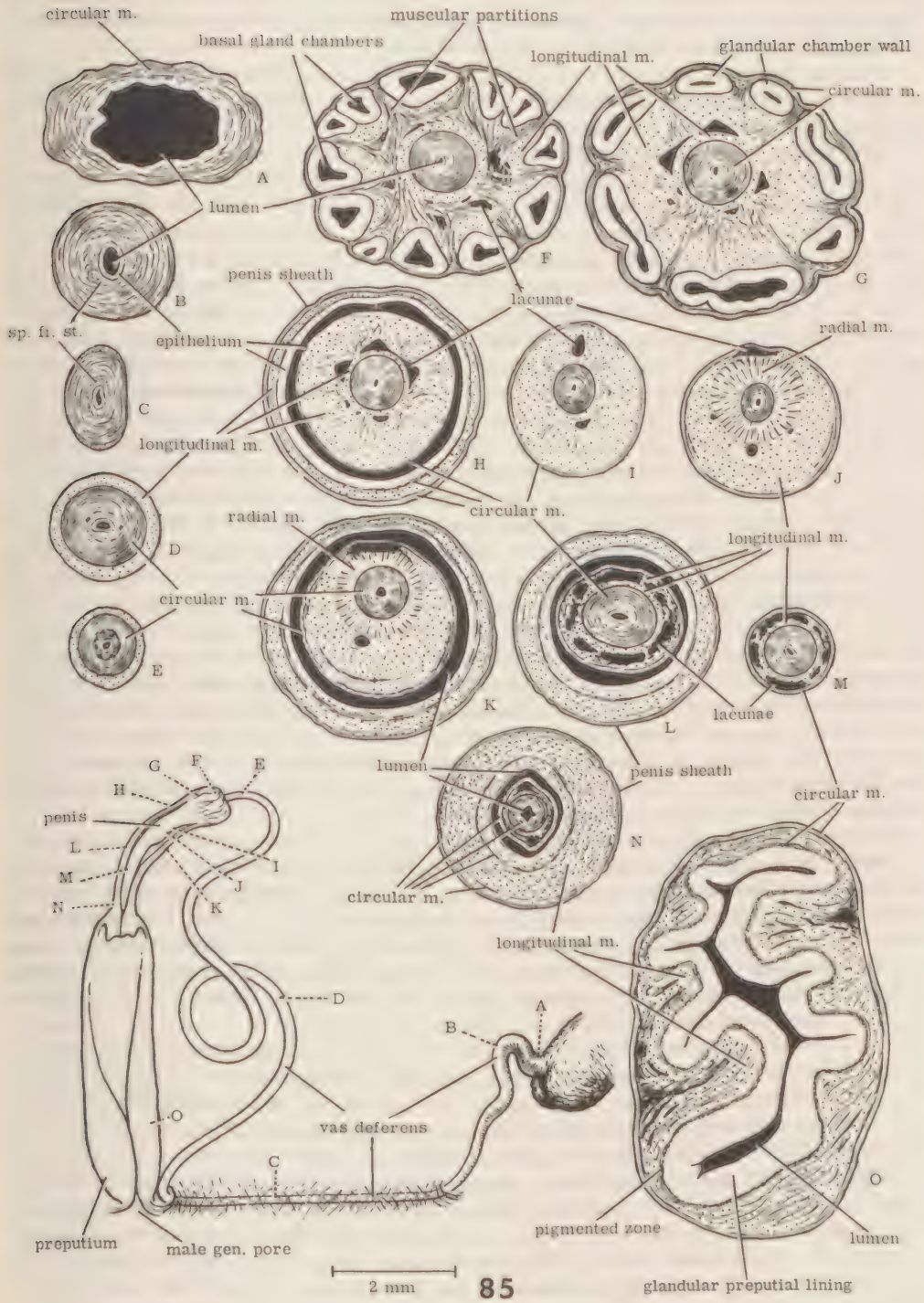
FIGURE 85. The vas deferens and penial complex, with sections of the same made at levels indicated by given letters. A penial complex of typical form is represented in the fully retracted posture. The sections represent thick slices of the tract as viewed by reflected light. Stippling indicates areas where cut ends of muscle fibers occur, either densely packed or spaced. The large slightly coiled bend in the initial wide portion of the vas deferens is a fixed, intrinsic feature. The vas consists of a posterior and an anterior division which differ in internal structure. The posterior division extends from the prostate to the base of the preputium, and it lies in the body wall for much of its length. It is smooth, mostly rather flattened, relatively weak in consistency, of relatively loosely organized tissue, and it has somewhat slight longitudinal musculature. The anterior division has a strong external layer of longitudinal musculature: it has a decided firmness and it tends to be minutely kinky. This division is that portion of the vas which extends from the base of the preputium to the sheath of the penis, while looping in the cephalopedal hemocoel. The part of the posterior division in the body wall fits closely in a canal which lies next to the lateral cervical sinus, from which it is separated by a thin musculomembranous wall (cf. Figs. 34 and 49). The vas in the body wall is so uniform in structure along its length that any section of it would be essentially identical to section C. For about the middle third of its length it is sheathed in a thin sleeve of longitudinal and criss-crossing muscle fibers which is part of the vas protractor (cf. Fig. 81). At the level of section C, and anterior to that, the sleeve is split longitudinally; it would appear as a C-shaped line largely surrounding section C if it were shown. It arises from the surface musculature of the vas about half way between levels B and C. The longitudinal muscle layer arises at about the same level as the sleeve, and in effect, the protractor is inserted there. As the vas leaves the body

wall anterior to level C, its longitudinal muscle layer rapidly thickens. Any section made between the point of exit and level D would be almost identical to section D.

Throughout the vas, beginning at level B, the circular muscle layer is separated from the central cylinder of epithelium by a loose stratum (sp. fi. st.) of fibers. In such thick sections this stratum cannot be seen very clearly, but it has a spongy-fibrous appearance. Where it is most evident (levels B to D), it is made up of separated fibers which seem to split off from the circular muscle layer, and pass to the epithelium following a curving course. These fibers form a criss-crossing pattern. In the anterior division of the vas, this stratum is invaded by several longitudinal cavities (section D) which enlarge in the anterior end of the vas (section E) and displace most of the fibrous tissue. Observations of the living vas by transmitted light revealed that the epithelium is suspended by the fibers as a tube in a substantial cavity, and indicated that the fibers are semispirally arranged. The epithelial tube is twisted spirally, it is irregularly convoluted along its length, and it is suspended very loosely in the terminal end of the vas.

In the anterior division of the vas, the longitudinal muscle layer is composed partly of many minute, short bands which split off from its surface, and then insert further along the vas (the basic arrangement of each such band is comparable to that shown in Fig. 81 for the vastly grosser component of the vas retractor which spirals along the tract). These bands occur all along that division in a close, irregularly staggered succession. In physiological salt solution, contractions of these bands are observed to cause a semispiral "knotting up," or kinking, at all points along the anterior division of the vas. The bands must be tensed at most times, since the kinking is almost always detectable, even in preserved specimens. In life, in no connection with mating activity, the vas unceasingly jerks pulsatingly at a rate of about one jerk per second. This action persists indefinitely in short segments cut from the vas. Each jerk results from a simultaneous contraction of many muscle bands and from the coincident kinking action. The vas pulls backward slightly away from its anterior end with each jerk, and at the same time the spirals of its epithelial tube are enhanced and forced against each other. Each jerk is accompanied by compression of fixed, short portions of the epithelial tube, and by the appearance of a series of expansions alternate to these. Between jerks, as the vas tends to unkink, the epithelial tube tends to uncoil, its compressed sections expand, and it takes on a relatively uniform, wide diameter. The anterior end of the epithelial tube actually seems to whip as a result of the jerks. During these actions, the vas does not vary noticeably in diameter. Also, the circular muscles do not contract conspicuously; perhaps they come into prominent play only during mating, in protracting the vas and in pumping semen by strong waves of contraction. The epithelium of the vas is densely ciliated along its length, except that unciliated patches occur at scattered points. The cilia are very large. With each jerk of the vas they bend in the direction of the anterior end of the tract and beat strongly. Between jerks they become erect and beat slowly.

It appears that in male mating activity, sperm accumulate in great volume in the prostate in a dense mass having little fluidity (cf. Fig. 79). A twisted convoluted seminal "rope" of firm consistency has been dissected from the posterior division of the vas when it was alive. Yet, the semen is observed to issue from the penis in a quite fluid (although densely whitish) state, when an acting male's coital activity is interrupted (in water). The semen then issues for a short time, as if it were under a strong, steady fluid pressure. Perhaps the elaborate com-


circular m.
basal gland chambers
muscular partitions
longitudinal m.
glandular chamber wall
circular m.
A
lumen
F
G
B
penis sheath
lacunae
sp. ft. st.
epithelium
radial m.
C
longitudinal m.
H
I
J
circular m.
radial m.
longitudinal m.
D
circular m.
E
K
L
M
lacunae
lumen
penis sheath
circular m.
G
F
E
H
penis
L
M
N
I
J
K
N
circular m.
longitudinal m.
D
B
A
O
vas deferens
C
O
pigmented zone
lumen
preputium
male gen. pore
glandular preputial lining
2 mm
85

bined muscular and ciliary activity of the vas is necessary to conversion of massed sperm to a more fluid state, and to pumping it continuously over a protracted period into the female tract (cf. Fig. 91).

The vas deferens actually passes into the penial complex and forms the central component of the basal region of the penis. Lacunae in this region form an interrupted cylindrical space around this part of the vas, which is more loosely suspended there than is apparent from the figure. There is considerable room for the vas to coil or bend in that space (cf. Fig. 90). Both the penis and its sheath are bilaterally symmetrical, and have a more or less dorsal, greater curvature and an opposite lesser curvature. The penis sheath is not everted in copulation. It is quite extensile, however, and it probably functions in initiating eversion of the preputium, by elongation of its lower end (cf. Figs. 80 and 84). Contration of its circular muscles must cause this action. The sheath evidently functions primarily as a protractor of the penis when the penial complex is everted, in an action necessary to achievement of coitus. Contraction of its more abundant longitudinal musculature would draw its free end, or head, toward its opposite end. This action probably is necessary for the protrusion of the terminal portion of the penis from the sheath. The longitudinal muscle of the penis sheath mostly consists of coarse, separate, irregularly spaced fibers or bundles of fibers. These are embedded in a dense stratum of tissue which grossly resembles the buccal gland tissue of the proesophagus (cf. Fig. 6), and it seems to consist mostly of gland cells. Circular or semispiral muscle fibers, partly formed into thin, spaced layers, divide this stratum into concentric layers. The gland cells are progressively more evident toward the lower end of the sheath. In sections H, K, L and N, numerous fine broken ovals are drawn to suggest the appearance of the gland cells. The label "longitudinal M," applied to the penis sheath, refers to scattered cut ends of muscle fibers. Note that the sheath tends to have a thicker wall on its lesser curvature. Usually, when the sheath is fully retracted and in a curved posture, the wall on the lesser curvature is very thick and that on the opposite curvature is quite thin and almost membranous. The specimen represented in the figure probably is not atypical in this respect: the condition varies markedly with changes in posture of the sheath.

The epithelium of the penis sheath appears to be glandular and it is generally ciliated. It is continuous with thick gland-tissue lining the chambers at the base of the penis. The chambers (cf. Figs. 89 and 91) are of variable lengths and they mostly branch or evaginate so as to form blind pockets which tend to overlap each other. Each chamber opens into the lumen of the penis sheath by a large, wide slit between levels G and H. The slits are of varied size. The chambers evidently can be compressed by the circular muscles outward to them, and by radial or diagonal fibers which form partitions between them.

The lacunae in the muscle tissue of the penis seem to be in narrow communication with the cephalopedal hemocoel through their extensions through level F. This probably provides the passageway for venous blood leaving the penis. A fine artery, with a fine nerve, was traced to the entrance of the vas deferens into the penis sheath (cf. Fig. 81), but neither artery nor nerve was traced further. It is suspected that the lacunae partly represent expansions of that artery. In life, "calciferous concretions" which look like those associated with arteries generally can be seen in the lacunae. The lacunae may be in part sinuses supplied with blood by the conjectural artery. The fine "lacuna" shown in sections J and K as a tiny black oval next to the radial muscle may be a branch of such an artery which delivers blood to the highly lacunar terminal half of the penis. The broad superficial lacuna on the greater curvature of the penis, revealed in the same sections,

may be the outlet for blood leaving the terminal penial region. The fine venous outlets at the head of the penis sheath probably can be closed by muscular action so as to lock blood within the penis, while their narrowness otherwise would help to maintain blood turgor.

The longitudinal muscle making up most of the penis, as revealed in Sections G to K, is exceedingly dense. The radial muscle shown in Sections J and K is also very dense; it is very strongly attached to the musculature contiguous to it, especially to the cylinder of circular muscle which surrounds the central epithelial canal. Radial fibers (shown in sections F to I, but not labelled) also occur in the base of the penis. These largely appear to arise from the partitions between the gland chambers, and to attach to the portion of the vas deferens lying in the penial base and to the central cylinder of circular muscle in the vas. The fibers of the dense radial muscle at the midlength of the penis angle away from the central cylinder toward the anterior end of the penis, while the weaker, more diffuse radial fibers in the penial base angle in the opposite direction (cf. Fig. 89). The latter fibers then are positioned to act as retractors of the central cylinder (and of the vas), while the former are positioned to act as protractors. The radial muscle could also act in dilating the central muscle cylinder and the penial lumen. However, opposing actions of that of the penial base and the penial midlength would tend to stretch and narrow the cylinder in the region from H to J. The indicated narrowing of the cylinder and of the penial lumen in that region is a characteristic feature of the penis. The enlargement of the central cylinder of circular muscle in the terminal region revealed in section L, the looseness of tissues around it, and the correlated enlargement of the lumen suggest that that region functions in accumulating amounts of semen momentarily and in propelling them from the penis with force. Delivery of amounts of semen to the terminal region probably is regulated by alternating constriction and dilatation of the penial lumen preceding that region in correlation with forward and backward shifting of central muscle cylinder. Contractions of both the central muscle cylinder and the radial muscle must contribute to these actions.

The penis has a very thin external epithelium. Cilia were not detected within or on the organ. It is highly mobile, quite extensile, and capable of wormlike, directed action. The swelling on the lesser penial curvature represents the male component of a copulatory holdfast mechanism (cf. Fig. 91). It is here called the penial knot. It is a transverse elevation which extends on to the lateral surfaces of the penis. In section K, a separation of a longitudinal muscle stratum in the knot is indicated. This stratum is largely confined to the knot, in which most of its fibers must originate and insert. The knot can be elevated as a rather steep ridge, evidently through action of these fibers. The tip of the penis as figured tends to be finned on opposite sides, but this partially may be an artifact due to shrinkage in preservative.

The preputium consists largely of musculature which is complexly, but rather loosely, organized. That intrinsic musculature primarily functions when the preputium is everted and controls and effects wormlike actions of the organ (cf. Figs. 84 and 91). When the organ is everted, its glandular epithelial lining forms its outward surface. That surface then shows no folds, although it may be elevated transiently during retractive movements of the organ to form regular, spaced annuli. Such annuli generally appear only in the distal third of the organ. When fully extended, the everted organ is about 3 times as long as it is when it is retracted. Then its musculature, as a whole, is longitudinally spread out or stretched, and forms a relatively shallow stratum on the inner preputial surface. The arrangement of the various components of the musculature probably can be

determined accurately in the organ only when it exhibits this condition. When the preputium is retracted, its large amount of muscle ceases to serve its essential function and must be "stored" by being crowded into a much shortened organ. Then, various groups of muscle fibers become bunched up and "tucked away" in a complex set of folds which develop on the inner epithelial wall of the organ (cf. Fig. 86). There are many irregularities in the folding which probably develop haphazardly. It is doubtful whether the pattern of folding is exactly duplicated in a given specimen, on successive retractions of the organ. When the preputium is retracted, its inward wall shows 2 primary longitudinal folds, one more or less posterior, the other nearly anterior. Extrinsic tensors (cf. Figs. 80 and 81) which insert along these folds must generally exert a pull on the posterior and anterior sides of the organ, so that its mesial and lateral sides tend to become flattened. The flattened effect is evident in the figure (section O). The upper portion of the organ is more roundly columnar. When fully retracted, the preputium is always "pinched in" at its base by closure of the male pore.

Most of the intrinsic preputial muscle seems to be neither quite "circular" or longitudinal. The labelled superficial "circular" muscle is made up of numerous coarse to fine separate strands which mostly do not completely encircle the organ, and tend to follow a semispiral or diagonal course. Those strands are arranged close together along the organ so as to form a loose, somewhat sleeve-like stratum. This stratum sends off many fibers which become involved with the deeper musculature. Two rather diffuse tracts of fibers which largely lie in the 2 primary longitudinal folds, make up a prominent part of the preputial musculature. These tracts are made of more or less longitudinal fibers, but only the more strictly longitudinal of these are abundant and well-massed together in the third of the preputium next to the male pore. These tracts functionally originate at the male pore. Fibers in the body wall converge toward the pore from all directions (cf. Fig. 49) and pass into the preputium, where they become longitudinally oriented as part of the 2 primary tracts. Many fibers diverge from these tracts all along their length; many fan out, or curve away markedly from the tracts. The diverging fibers are grouped irregularly into diffuse diagonal and even "swirled" tracts, which partly seem to merge with similar tracts. The grosser, divergent groups of fibers tend to follow large secondary folds which split off from the 2 primary folds. Lesser fiber-groups mostly issue more or less transversely from the primary and secondary folds, and those coming from one fold tend to interdigitate with those coming from adjacent folds. Some more or less longitudinal fibers pass from the general musculature in the portion of the preputium adjoining the penis sheath and attach in the velum and on adjacent tissue of the sheath. Perhaps these fibers are direct extensions of the 2 primary preputial muscle tracts.

There is a considerable amount of space filled with blood in the preputial wall. This space consists of innumerable fine spaces between the muscle fibers, and of 2 rather large spaces in the 2 major folds. A delicate membrane apparently invests the organ and weakly locks venous blood in its wall. There undoubtedly is an extensive arterial complex within that wall, especially on the mesial side of the preputium, but it was not studied. Numerous densely white "calciferous concretions" occur on the upper mesial side of the organ and deep among the muscle masses in that region, and in the major and minor folds. The luminal wall of the preputium is lined with a thick stratum which seems to be glandular. To what extent this stratum is made up of epithelium is unknown. That epithelium, especially in the basal half of the organ, is well-ciliated.

FIGURE 86. The retracted preputium of a preserved, previously narcotized snail, A, and of a drowned specimen, B (cf. Fig. 85). Both organs are from adults and have been cut open longitudinally and flattened to reveal their inner surfaces and the 2 rings formed by the velum and sarcobellum (cf. Fig. 87) around the outlet of the penis sheath. The coarseness of the folds in example A seems to have been caused by the tensing or contraction of muscle elements in the organ and by condensation and shrinkage of tissues resulting from preservation. Note how a serrated pattern forms where some folds lie next to each other, indicating that under the epithelium a series of diagonal groups of muscle fibers issue from the edge of one fold and interdigitates with a similar series issuing from the adjacent fold. The wall of example B is smoother than the drawing seems to suggest; the folds have been delineated strongly to emphasize their pattern. In this example the muscles seem to be about as relaxed, and the folding about as minimal, as is possible in the retracted organ. If contracted and "condensed," this example would closely resemble example A. The indicated muscle fibers were demonstrated by transmitted light. Note how they form 2 main tracts. The shown fibrous extensions of them at the lower end of the organ insert in the body wall of the snail, around the male pore (cf. Fig. 49).

FIGURE 87. The velum and sarcobellum of the penial complex of 3 adult specimens, in longitudinal sectional views of the region of juncture of the penis sheath and preputium, in the retracted penial complex. The velum and sarcobellum are bright yellow in life, which suggests that they are glandular. Perhaps they give off a secretion which is excitatory to the acting female in mating. The sarcobellum may be essentially a sensory structure having a special sensitivity to the lips of the female pore. The velum seems to provide a place of insertion of some fibers of longitudinal muscle tracts of the preputium. The sarcobellum seems to provide the place of insertion for fibers of the extrinsic preputial retractor, part of which is shown in example B, and the place of origin of some of the longitudinal musculature of the penis sheath (cf. Figs. 85 and 91). Evidently the velum is capable of altering its size and form considerably by muscular action. The sarcobellum is a fleshy ring around the outlet of the penis sheath, and ordinarily it is hardly identifiable morphologically. In example A it is more well-defined than in any other example observed. The same preparation also shows the most enlarged and extended velum ever seen in the population studied. In this case, these structures actually were found to be surrounding the penis, which was extended from its sheath (the penis was removed in dissection). This example, like example B, shows an asymmetrical condition of the velum in which one side is more prolonged than the other. This condition is often seen in "narcotized" snails; it tends to be associated with the earliest stage of inversion of the preputium into itself, and it probably depends very much on the action of the preputial retractor. In this condition the velar edge often is split or irregularly lobed. Example B illustrates an early stage of preputial inversion and example C shows a slightly more advanced inversional stage. In the latter the velum and sarcobellum are in a "resting" or fully retracted state, which is usually seen in the pre-inversion posture and in later stages of inversion and eversion. In the latter 2 examples, the outlet of the penis sheath was actually found to be closed (the common condition), but the sheath has been spread open somewhat in dissection so as to expand that outlet.

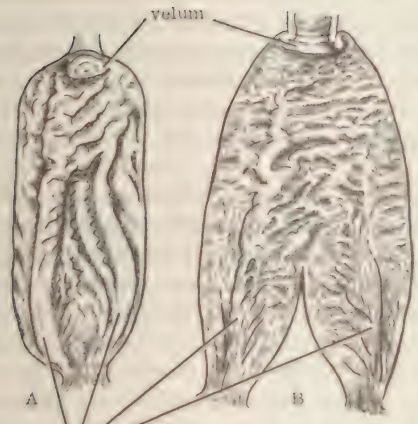
FIGURE 88. A full face view of the structure formed by the sarcobellum and velum at the juncture of the penis sheath and preputium (cf. Fig. 87). In this example,

the outlet of the penis sheath, in the center of the sarcobellum, is closed, as is usual except during copulation. In its intrinsic shape, the structure is actually quite discoidal, but commonly and normally it becomes distorted by pressure of the preputial wall when it is being protracted in the inversion process. The example shown was fixed within the preputium in a distorted condition when it was preserved. The edge of its velum, shown to the left, is somewhat prolonged and bent backward. When the penial complex is everted it has a truncate free end which is capped by the velar-sarcobellar structure (cf. Fig. 91).

FIGURE 89. The penis dissected to clarify its internal structure, and the head of the penis sheath with the gland chambers represented somewhat diagrammatically (cf. Fig. 85). The lumina of the chambers are represented in black as showing through the surface tissues. The penis is represented as having all of its tissues removed from one side along its length to the central circular muscle cylinder. This example of the penis exhibits a form which may be taken as the resting intrinsic one, characteristic of the population it represents. It is neither especially retracted, contracted or extended.

FIGURE 90. The penis of 4 adult specimens in side view illustrating observed variants of form. Examples A and D were dissected from live specimens, and examples B and C were taken from preserved, previously "narcotized" specimens (cf. Figs. 85, 89 and 91). The variation largely represents effects of contractile and extensile actions of the organs. Example A shows how the continuation of the vas deferens into the penis may coil up in the lacuna in the penial base. This happens when the penis is retractively contracted. Example B shows a highly retracted condition. However, the penis may be even more contracted and massively compressed against its base; the penial knot then is thrown up into a narrow transverse ridge that is tightly pressed back against the penial base so that it becomes difficult to discern. Example C exhibits an artifact in having an expanded tip. In that case, the penis was found to have been extended into the preputium by protraction of its sheath. The sheath had closed around and constricted the shaft of the penis short of the penial tip, and preservation fixed the tissues in this relationship (cf. Fig. 83). Example D shows a moderately extreme extended condition, in which the coil of the vas deferens in its vas has straightened out. On further elongation, the contour of the penial knot becomes very obscure. The central cylinder of circular muscle is indicated in examples A and D. Note that it is much narrowed in the region of the penial knot. The penis is pale yellow, cream color, or almost colorless in life. Visually, in life the middle region of the penial length is markedly set off from adjacent parts of the penis, because its musculature is especially massive, especially shiny-reflective, and opaque. By transmitted light, that region contrasts darkly with less dense, more translucent parts of the organ. The region is further set off by the near lack of white "calciferous concretions," which are numerous in the lacunae of the penial base and the terminal division of the organ.

FIGURE 91. The advanced stagnicoline copulatory holdfast mechanism as exhibited by 2 specimens of the "*elodes*" Say form of *L. catascopium* in coitus. Attempts to make a comparable preparation from specimens of the "*angulata*" population represented by the other figures were not successful. Nevertheless, the figure can be taken in all details as representative of that population. The penis sheath and preputium are shown in longitudinal sectional view and the female structures are represented as being transparent. To make the preparation, the



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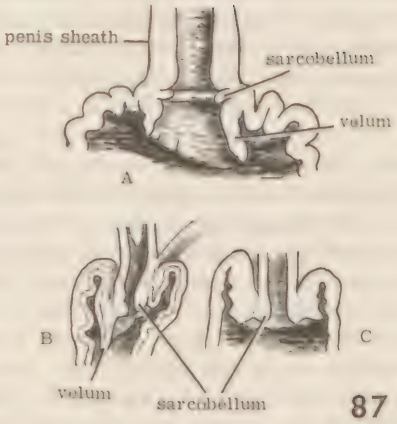

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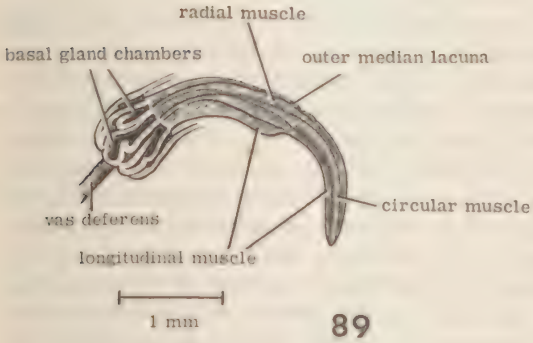

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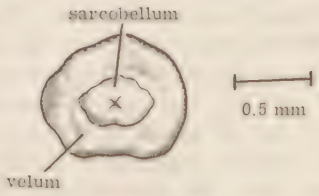

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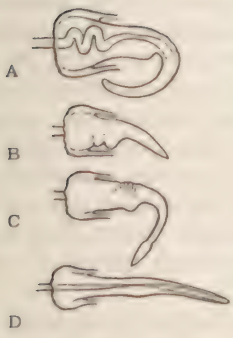

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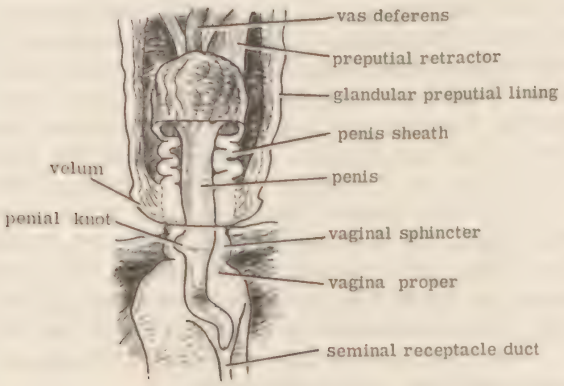

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preputium of the living acting male was severed, which left the penis locked in the female tract with the penis sheath and the terminal region of the preputium appended to it. The acting female was then preserved, and afterwards, the organs were dissected. The acting female represented here was relatively small, and perhaps subadult; its shown parts are less robust than in large adults. When it is attempted to separate an *in copula* mating pair, the male and female organs usually strongly resist being pulled apart.

In activity preliminary to coitus, the acting male usually takes up a position on the right side of the shell of its mating partner, with its anterior end pointing in the same direction as that of the partner. The male pore of the former then is far anterior to, and well above, the female pore of its mate, on a diagonal line. In large adults, the distance between those pores then is about 15 mm. On eversion, the preputium undergoes highly mobile, wormlike activity, and it makes contact with the female pore through blind "seeking" behavior, in which the penis occasionally is thrust against the integument of the acting female in a probing action. The truncate end of the penial complex seems to have a special sensitivity to the lips of the female pore, for the "seeking" abruptly ceases, and the penis is abruptly inserted when it makes contact with those lips. The sensitivity probably largely lies in the sarcobellar tissue, which exactly fits against the lips of the pore during coitus, as shown. Those lips are markedly yellow in color, which may suggest that they secrete a stimulatory substance.

In view of the shortness of the penis relative to the length of its sheath (cf. Figs. 51, 85 and 90), and on consideration of details of the posture of male parts in this figure, the question of how penial anchorage in the female tract is achieved becomes rather complex. It is apparent that protrusion of the tip of the penis is brought about by shortening of the penis sheath, which becomes folded accordion-like in the process. It may be doubted, however, that it can shorten as much as is indicated here, by its own action and before the penial knot is anchored in the female tract. It appears from the figure that extreme shortening of the sheath depends on its being compressed by a pulling action on the part of the anchored penis. Here, the penis shows an elongately cylindrical condition of its basal half which may exist only during coitus. Because of the lack of strong constrictor muscles in the penis, it is doubtful that that penial region can be so prolonged by its own activity alone. The drawing may suggest that the condition results from that region either being stretched by the head of the penis sheath exerting a pull away from the anchored knot, or from being compressed by the walls of the sheath. It would seem that the latter action would tend to extrude or squeeze the penis out of the sheath. It may be that this action is necessary to protruding the penis so far as to expose its knot. Perhaps, however, the knot is pulled from the sheath by the penis. It might do so if its tip acquired preliminary anchorage in the vagina, by hooking actions aided by contractions of the vaginal sphincter. Then, the penis sheath may be enabled to exert a greater extrusive action. The penial tip might then penetrate more deeply, and by a hooking action and contraction it may pull the knot to the point where the vaginal sphincter may clamp around it. The knot apparently is enabled to become especially well-elevated once it gains purchase in the sphincter.

It seems likely that during coitus the basal half of the penis undergoes repeated contractions, which would contribute to pumping semen into the duct of the seminal receptacle. Such an action could aid in forcing a secretion out of the gland chambers onto the penial surface, and out of the sheath onto the lips of the female pore. The secretion (which has not been observed) probably stimulates cooperative actions of the acting female and of its vaginal sphincter. On examin-

ing a number of acting females after interrupting their copulatory activity, in some the duct of the seminal receptacle was found to be filled with sperm and much expanded thereby, but in some, sperm was found in the lower vaginal tract. Peristaltic waves of the receptacular duct probably carry the sperm placed in it to the receptacle during or soon after mating. Probably some sperm usually spills over or is inadvertently misplaced into the vaginal tract during mating. Coitus commonly lasts well over an hour.

The copulatory holdfast mechanism is generally lacking in Old World lymnaeids, and it is poorly developed in primitive stagnicoline species. As illustrated here, it characterizes *Lymnaea catascopium* and its near relatives; along with the prostate pouch and bicuspid lateral teeth it marks these snails as advanced stagnicoline, or higher, Lymnaeidae.

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[3]Obtainable from University Microfilms, Ann Arbor, Michigan, U. S. A.

ADDENDUM

After this work had gone to press, some changes and additions to the manuscript came into consideration but could not be made. The pertinent considerations are noted below.

It was not sufficiently appreciated until after the figures were captioned that the highly glandular reproductive organs of the specimen represented in Figs. 58-60, 65-68, 79, 85 (and some other figures), were considerably reduced in size, and that the snail at some time probably had had a trematode infection of unknown magnitude. This reduced size must be considered in referring to the scales given in reference to that specimen. However, it should be emphasized that, except for size, the figured features of this snail's organs did not differ from normal specimens with which it is compared. It may even be that the reduced condition was partly the effect of recent oviposition, rather than of the infection. It is to be noted especially that the oviducal cecum of the specimen, in the given state (cf. Fig. 58), would seem to be too small to contain and mould a normal-sized egg-capsule (cf. Fig. 51), and that it's labyrinth and the uterine

cecum evidently are too small to function quite as was suggested, in the transport of capsules of such size.

The size of the albumen gland compared to that of the egg capsule is pertinent to matters referred to in several figure captions. The largest albumen gland recorded (cf. Figs. 51, 71) is roughly equivalent in volume to 40 capsules (largely consisting of "albumen"). Since 100 capsules (and often well over 40) of normal size can occur in an egg mass, and since all capsules within a mass evidently are formed within a period of a few hours (even minutes?), the gland would appear to have the amazing capacity to produce a quantity of "albumen" more than twice as great as itself in volume within such a period. This view would be modified if the capsules swelled significantly after deposition, but I am fairly certain that this does not occur. On the other hand, lymnaeid egg masses reportedly may increase more than 40% in volume in about a week's time following deposition. Also, the masses reportedly are largely self-attaching, and the snail is supposed to use it's mouth, but not it's foot, in aiding the attachment of the egg mass. It would then seem that nothing is added to the mass after it leaves the female tract.

It should be noted that in the literature, "egg capsule" may refer to what is here called the "egg mass," and that "ovum" is generally equivalent to "primary oöcyte" in my account. References to "nurse" cells here may be misdirected, but at least suggest that certain phenomena reported to occur in the lymnaeid gonad may need clarification. "Endogenous" and "exogenous" might well be substituted, respectively, for "selfing" and "crossing" in references to sperm made here. "Bursa copulatrix" might advisedly replace "seminal receptacle" here, on consideration of possible functions, and of probable homologies and non-homologies among gastropods. While a "pallial" connotation is avoided here in respect to the peristomial collar, it is accepted that the lung, in part, properly may be called "pallial" and be said to be lined with "mantle" epithelium. It would not seem proper, however, to apply these adjectives to the floor of the lung. Ciliation may be present in the lung of the snail described here, but it was not definitely detected.

The following additions should be made to the reference list:

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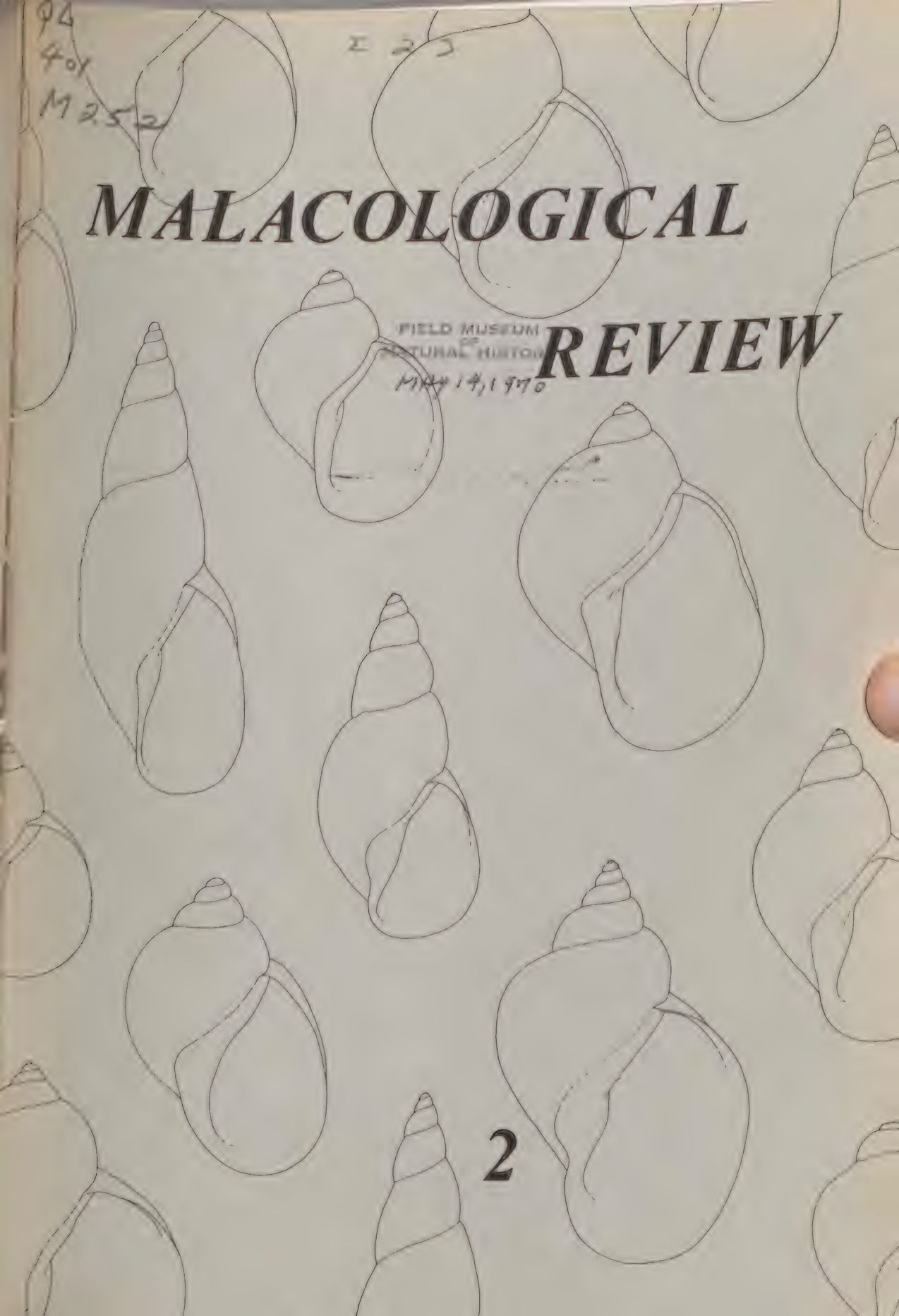

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SOME CHITONS FROM TAIWAN (FORMOSA)

Shi-Kuei Wu

ABSTRACT

Eight species of chitons have been recorded previously from Taiwan. The present paper deals with 6 species of relatively rare chitons, *Acanthopleura spinosa*, *Acanthochiton armatus*, *Cryptoplax striatus*, *Ischnochiton alatus*, *Liolophura gaimardi* and *Onithochiton hirasei*. *A. spinosa* and *O. hirasei* have been recorded previously; the other 4 species are reported for the first time.

Eight species of chitons have been recorded from Taiwan by Japanese workers (Taki, Is., 1938, 1947, 1962; Kuroda, 1941; Taki, Iw., 1964a, 1964b; Habe, 1965). These species are: *Ischnochiton comptus* (Gould), *Lepidozona coreanica* (Reeve), *Rhyssoplax komaiana* (Taki, Is. & Taki, Iw.), *Liolophura loochooana* (Broderip & Sowerby), *Acanthopleura spinosa* (Bruguière), *Acanthozostera gemmata* (Blainville), *Onithochiton hirasei* (Pilsbry) and *Nuttallina alternata* (Sowerby). The above species were only listed or illustrated with few words of description; no detailed study has been undertaken.

The present work, based on the collections made by the author during the years of 1963 to 1966 along the intertidal zone of the Taiwan coast line, describes 6 species of chitons that occur rather rarely around the island. Four of the species (*Acanthochiton armatus*, *Cryptoplax striatus*, *Ischnochiton alatus* and *Liolophura gaimardi*) are recorded for the first time from Taiwan.

The following account gives for each species the original description reference, published synonyms and distribution for Taiwan, collection locality in Taiwan, size and morphology of the valves, girdle and radulae, and the numbers and position of the ctenidia.

1. *Acanthopleura spinosa* (Bruguière, 1792)

Figs. 1 and 7-15.

Chiton spinosus Bruguière, 1792, p 25-28, pl. 2, figs. 1-2, A, B, C.
Acanthopleura spinosa, Kuroda, 1941, p 71. Ta-pan-lien (=Daizubo).
Acanthopleura spinosa, Taki, Is., 1962, p 47. Formosa.
Acanthopleura (*A.*) *spinosa*, Taki, Iw., 1964b, p 412. O-luan-pi (=Garanbi).

Collection locality: Wan-li-tong (1 specimen).
Size: Length 50 mm, width 40 mm.
Description: The valves are uniformly chestnut in color. The head valve (Figs. 7-8) is hemispherical, beaked, inconspicuously latticed and irregularly scattered with eyes. Its insertion plate is light chestnut color, long (about 1/3 of its valve length) and it has 18 slits; each tooth is grooved and pectinate. The interior of the head valve is dark purple. The intermediate valves (Figs. 9-10) are fan-shaped and beaked; their central areas smooth, their lateral areas inconspicuously latticed and scattered with eyes. The sutural plates are large and are connected with each other by the sinus plate. The sinus plate of the 2nd valve is distinctly pectinate, but the sinus plate of the other valves is obsolete. The insertion plates (or lateral teeth) of the intermediate valves are triangular and grooved, and usually have 1 lateral slit. The interior of the intermediate valves is white in the center

and chestnut colored at the posterior and posterio-lateral regions. The anal valve (Figs. 11-13) is kidney shaped: its central area is smooth and its posterior area is weakly latticed and scattered with eyes; the mucro is posterior. The sutural and insertion plates are coalesced; the latter is tall and has 10 slits; the teeth are grooved and pectinate; the interior of the anal valve is white-tinged with dark purple.

The girdle is wide (Fig. 1), covered dorsally with stout, black spines of various lengths (5-15 mm). It has relatively short (2-3 mm) spines at the margin, and square scales (Fig. 14) on the ventral side. There are 71 ctenidia on each side, extending from the mouth to anus.

Radula (Fig. 15): The central tooth (C) has a pentagonal base, somewhat bifurcated posteriorly; the cusp erects from the base by a narrow stalk. The central lateral tooth (CL) is winged and cusped and has a rectangular base. The major lateral tooth (ML) has a thick and stout shaft with a large projection at the medial side; the cusp is basin-like. The inner and outer small lateral teeth (ISL and OSL) are more or less triangular and are located under the cusp of ML. The major uncinus (MU) is a leaf-like blade projecting from a small rectangular base. The inner and median marginal teeth (IM and MM) are oblong or rectangular, and the outer marginal tooth (OM) is square.

Remarks: The species is characterized by: 1) head and anal valves having a long insertion plate with each tooth grooved and pectinate; 2) the sinus plate of the intermediate valves are pectinate (the 2nd valve is distinctly pectinate, but this condition in valves 3-7 is obsolete); 3) the proximal portions of the sutural plates are tinged with a chestnut color; and 4) long and strong spines are present on the dorsal side of girdle. The present specimen agrees with the description of Pilsbry (1893, p 220).

2. *Acanthochiton armatus* (Pease, 1871)

Figs. 2 and 16-23.

(?) *Acanthochites armatus* Pease, 1871, p 195.

Collection locality: Shi-tzu-wan (1 specimen).

Size: Length 14 mm, width 8 mm.

Description: The valves are yellowish brown with 2 or 3 black spots on each side of the dorsal areas except on the head and anal valves. The latter (Fig. 21) has a black spot on the sides of mucro. The head valve (Figs. 17-18) is hemispherical and radially striated. Its insertion plate has 5 slits. The intermediate valves (Figs. 19-20) are spherical or obtuse pentagonal and radially striated. The sutural plate is white; the insertion plate of the intermediate valves is triangular and has 1 lateral slit. The anal valve (Figs. 21-22) is spherical and striate; the mucro is located at the center of the valve. Its sutural plate is large; its insertion plate is tall and vertical, and has 1 lateral slit.

The girdle (Fig. 16) is wide, leathery, uniformly red-brown and has 9 elevated white setigerous pores on the sides of the valves. The setigers are long, fine and pointed. The ventral side of the girdle is covered with dagger-like scales (Fig. 23). There are 13 ctenidia on each side, located in that part of the pallial groove corresponding to the dorsal location of the 4th to 7th valves.

Radula: ML is 3-cusped.

Remarks: This specimen closely resembles *A. defilippi* (Pilsbry, 1893, p 19-20); however, it differs in having the girdle 1) "leathery" instead of "hairy" and 2) "white setigerous pore" instead of "black setigerous pore." The present species agrees rather closely with Pease's (1871) description of *A. armatus*.

FIGS. 1-6. Some chitons from Taiwan. FIG. 1. *Acanthopleura spinosa* (Bruguière), dorsal view. FIG. 2. *Acanthochiton armatus* (Pease), dorsal view. FIG. 3. *Cryptoplax striatus* (Lamarck), dorsal view. FIG. 4. *Ischnochiton alatus* (Sowerby), dorsal view. FIGS. 5a and 5b. *Liolophura gaimardi* (Blainville), dorsal view. FIG. 6. *Onithochiton hirasei* Pilsbry, dorsal view.

3. *Cryptoplax striatus* (Lamarck, 1819)

Figs. 3 and 24-36.

Chitonellus striatus Lamarck, 1819, p 317.

Collection locality: Shun-kuang-chuei (1 specimen).

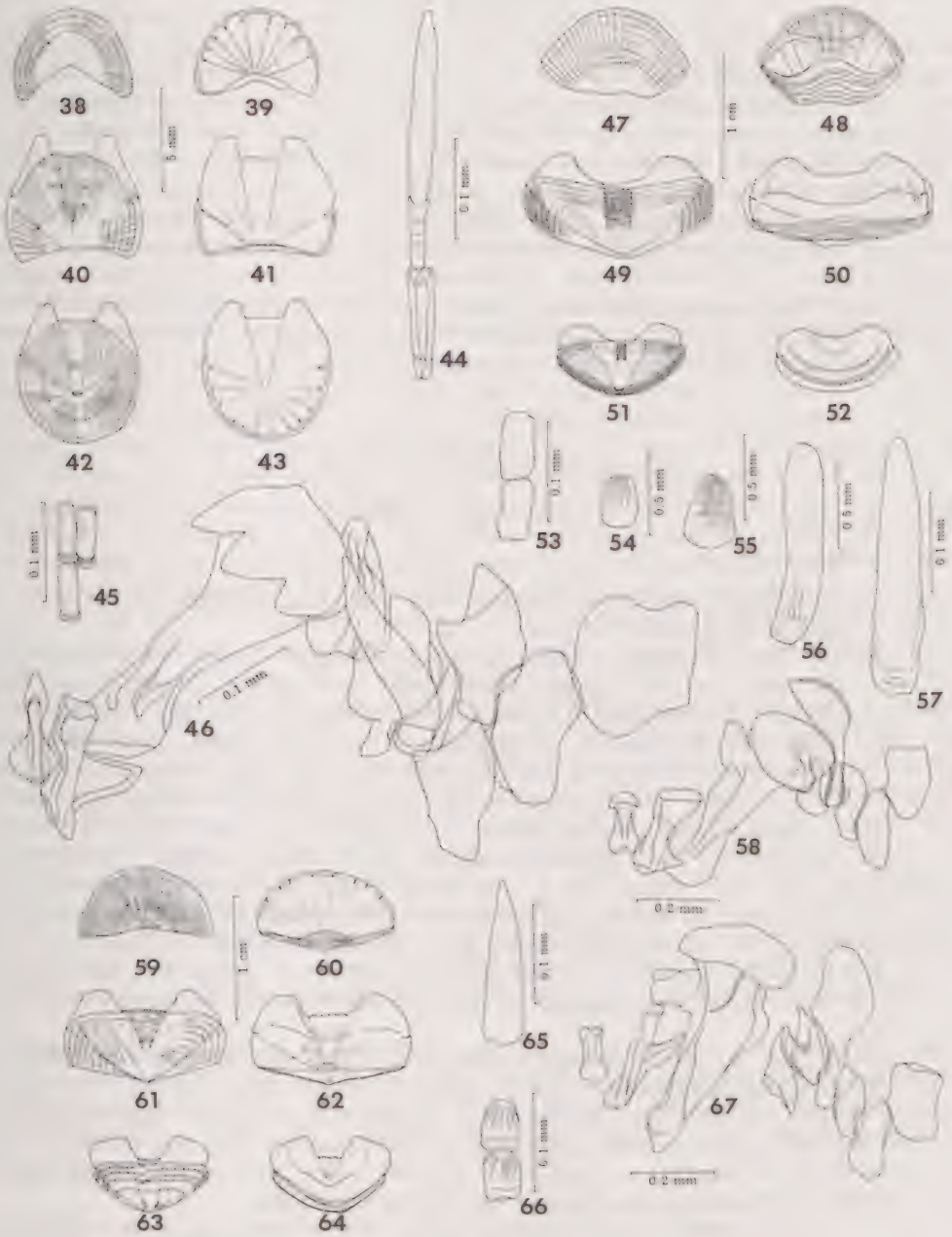
Size: Length 20 mm, width 7 mm.

Description: The body (Fig. 3) is vermiform and very convex dorsally. The valves are light brown in color. The head valve (Figs. 24-25) is horse-shoe shaped; its insertion plate has 3 slits. The intermediate valves (Figs. 26-28) are elongate-oval shaped (width 1/3 of its length); their dorsal areas smooth, their central areas longitudinally grooved and inconspicuously granulated. The sutural plates are small. There is no lateral slit or lateral tooth present. The interior of the intermediate valves is white, and porous in the middle. The anal valve (Figs. 29-31) is oval and arched; its sculpture like that of the intermediate valves; the mucro is posterior and terminal.

KEY TO LETTERING, FIGS. 7, 9, 11, 15, p 106

B	= beak	MM	= median marginal tooth
C	= central tooth	MU	= major uncinus
CA	= central area	OM	= outer marginal tooth
CL	= central lateral tooth	OSL	= outer small lateral tooth
I	= insertion plate	PA	= posterior area
IM	= inner marginal tooth	SI	= sinus plate
ISL	= inner small lateral tooth	SL	= slit
LA	= lateral area	SR	= slit ray
M	= mucro	SU	= sutural plate
ML	= major lateral tooth		

FIGS. 7-15. *Acanthopleura spinosa* (Bruguière). 7-8, Head valve, dorsal and ventral views; 9-10, An intermediate valve, dorsal and ventral views of 3rd valve; 11-13, Anal valve, dorsal, ventral and posterior views; 14, Ventral scales of girdle; 15, Radula, dorsal view. FIGS. 16-23. *Acanthochiton armatus* (Pease). 16, Dorsal view of *A. armatus;* 17-18, Head valve, dorsal and ventral views; 19-20, Intermediate valve, dorsal and ventral view of 5th valve; 21-22, Anal valve, dorsal and ventral views; 23, Ventral scales of girdle. FIGS. 24-36. *Cryptoplax striatus* (Lamarck). 24-25, Head valve, dorsal and ventral views; 26-28, Intermediate valve, lateral, dorsal and ventral view of 6th valve; 29-31, Anal valve, lateral, dorsal and ventral view; 32-34, Dorsal spicules of girdle; 35, Ventrolateral scale of girdle; 36, Radula, dorsal view. FIGS. 37-46. *Ischnochiton alatus* (Sower-



by). 37, Dorsal spicule of girdle; 38–39, Head valve, dorsal and ventral views; 40–41, Intermediate valve, dorsal and ventral views of 7th valve; 42–43, Anal valve, dorsal and ventral views; 44, Marginal spicule of girdle; 45, Ventral scales of girdle; 46, Radula, dorsal view. FIGS. 47–58. *Liolophura gaimardi* (Blainville). 47–48, Head valve, dorsal and ventral views; 49–50, Intermediate valve, dorsal and ventral views of 6th valve; 51–52, Anal valve, dorsal and ventral views; 53, Ventral scales of girdle; 54–56, Dorsal spicules of girdle; 57, Marginal spicule of girdle; 58, Radula, dorsal view. FIGS. 59–67. *Onithochiton hirasei* Pilsbry. 59–60, Head valve, dorsal and ventral views; 61–62, Intermediate valve, dorsal and ventral views of 6th valve; 63–64, Anal valve, dorsal and ventral views; 65, Dorsal spicule of girdle; 66, Ventral scales of girdle; 67, Radula, dorsal view.

The girdle (Fig. 3) is wide, densely covered dorsally with 3 kinds of spicules: 1) long, straight and flat spicules (Fig. 32), 2) medium, curved spicules (Fig. 34), and 3) short and curved spicules (Fig. 33). All the spicules are grooved and ridged. The ventrolateral side of the girdle is covered with dagger-like scales (Fig. 35). Thirteen ctenidia are present on each side, located in that part of the pallial groove corresponding to the dorsal location of the 6th to 8th valves.

Radula (Fig. 36): The central tooth has an oval-shaped cusp erected from a rectangular base which is bifurcate posteriorly. The central lateral tooth is winged with a triangular base. The major lateral tooth is 3-cusped. The cusp of the major uncinus tooth is pectinate and projects from the rectangular base through a long stalk.

Remarks: The present specimen is identical to Pilsbry's figure for *C. striatus* (Pilsbry, 1893, pl. 11, fig. 38) and Reeve's figures (Reeve, 1847, figs. 4, 5 and 7) for *C. striatus*, *C. rostratus* and *C. oculatus*.

4. *Ischnochiton alatus* (Sowerby, 1841)

Figs. 4 and 37-46.

Chiton alatus Sowerby, 1841, p 61.

Collection locality: Nan-fan-ao (1 specimen), Wan-li-tong (1 specimen).

Size: Length 30 mm, width 13 mm.

Description: The body (Fig. 4) is long. The valves are brownish and delicately marbled with olive or olive-green. The head valve (Figs. 38-39) is crescent-shaped and radially granulated. Its insertion plate has 9 slits. The interior of the head valve is white with tinges of light pink and brown near the apex. The intermediate valves (Figs. 40-41) are pentagonal shaped: their central areas have longitudinal ridges; their lateral areas are decidedly raised and irregularly granulated. The sutural plates and the lateral tooth are small; the valve has 1 lateral slit. The interior of the intermediate valves is white but has 2 pink-colored patches in a wide "V" shape. The anal valve (Figs. 42-43) is subspherical, the mucro is at the center of the valve: its central area is elevated and longitudinally granulated except in the middle region which is only striated; its posterior area is flat and radially granulated. The sutural plates are small and the insertion plate has 8 to 12 slits. The interior of the anal valve is white tinged with pink at the center.

The girdle (Fig. 4) is the widest at the level of the 4th valve and narrowest at the anterior and posterior ends. The girdle is covered with: 1) thick, curved and ridged spatulate spicules (Fig. 37) dorsally, 2) spicules with cup, ring and formative cell (Fig. 44) at the margin, and 3) rectangular scales (Fig. 45) on the ventral side. There are 39 ctenidia on each side, located in that part of the pallial groove corresponding to the dorsal location of the 2nd to 8th valves.

Radula (Fig. 46): The central tooth has a tiny cusp projecting from a diamond-shaped base. The central lateral tooth has a triangular base with a small cusp at the dorsolateral corner. The major lateral tooth is 3-cusped. The major uncinus tooth is pointed and not expanded into a leaf-like blade.

Remarks: The present specimens agree with the descriptions of Pilsbry (1892, p 60) and Reeve (1847, species 45). The spicules and scale of the girdle are identical with those described by Leloup (1937, p 165).

5. *Liolophura gaimardi* (Blainville, 1825)

Figs. 5a, 5b and 47-58.

Chiton gaimardi Blainville, 1825, p 546.

Collection locality: Yeh-liu (1 specimen, Fig. 5a), Wan-li-tong (1 specimen, Fig. 5b), Shun-kuang-chuei (1 specimen).

Size: The largest specimen (Fig. 5a) (Yeh-liu) measures: Length 32 mm, width 20 mm.

Description: The valves are chestnut-colored, mostly with 2 median white bands, except the head valve is without a band. The head valve (Figs. 47-48) is hemispherical and inconspicuously granulated. Its insertion plate has 9 slits; the teeth are pectinate. The interior of the valve is dark grey with an oval black patch in the mid-anterior region; the slit rays are distinct. The intermediate valves (Figs. 49-50) are more or less rectangular with rounded angles: their central areas have wavy growth lines, their lateral areas have 5 radially granulated rows and are scattered with eyes. The sutural plates are rounded anteriorly and connected with each other by a sinus plate; the lateral tooth is pectinate and has 1 lateral slit. The interiors of the intermediate valves are white, except for the transverse callus ridge which has light chestnut color. The anal valve (Figs. 51-52) has a low triangular shape; its posterior area is small and inconspicuously granulate; the mucro is posterior. The sutural plates are rounded anteriorly and more or less connected to each other by a sinus plate. In the place of the insertion plate is a crescentic callus ridge. Both sides of the callus ridge are slightly pectinate. The interior of the anal valve is a light chestnut color at the mid-anterior region and on the crescentic ridge.

The girdle (Fig. 5b), tessellated with white and dark brown bands, is covered with spicules of about 1.5 mm in length (Fig. 56). There are 2 kinds of dorsal spicules: 1) short, flat, thick and striate (Fig. 54), and 2) conical (Fig. 55). The spicules at the margin have blunt tips (Fig. 57). Rectangular scales (Fig. 53) occur on the ventral side. There are 32 ctenidia on each side, located in that part of the pallial groove corresponding to the dorsal location of the 2nd to 7th valves.

Radula (Fig. 58): The central tooth has a triangular base with the posterior margin bifurcated; the cusp projects from the base by a narrow stalk. The central lateral tooth has a wing, cusp and rectangular base. The major lateral tooth has a basin-like cusp and a projection on the medial side of its strong shaft. The major uncinus tooth has a leaf-like blade which connects to the small base by a stalk.

Remarks: The present specimens agree with the species described by Pilsbry (1892, p 240-241, pl. 53, figs. 30-35). Pilsbry (1892) pointed out the differences between this species and the genus *Acanthopleura*. However, the radula of the present specimen (Fig. 56) is basically similar to that of *Acanthopleura spinosa* (Fig. 15).

6. *Onithochiton hirasei* Pilsbry, 1901

Figs. 6 and 59-67.

Onithochiton hirasei Pilsbry, 1901, p 203-204.
Onithochiton (*Onithoplax*) *hirasei*, Kuroda, 1941, p 71. Chi-lung (=Kiirun), Mu-tan-wan (=Botanwan). Peng-hu (=Hoko).
Onithochiton hirasei, Taki, Is., 1947, p 1269, fig. 3608. Taiwan.
Onithochiton (*Onithoplax*) *hirasei*, Taki, Is., 1962, p 47-48. Formosa.
Onithochiton (*Onithoplax*) *hirasei*, Taki, Iw., 1964b, p 412. Taiwan.
Onithochiton hirasei, Habe, 1965, p 216, pl. 66, fig. 4. Taiwan.

Collection locality: Shun-kuang-chuei (1 specimen).

Size: Length 28 mm, width 22 mm.

Description: The valves are greenish-brown; the central areas of the intermediate and anal valves have a white triangular patch variegated with dark brown. The head valve (Figs. 59-60) is hemispherical, radially granulated and scattered with black eyes which are arranged in 12 primary radii. Its insertion plate has 8 slits and each tooth is pectinate. The interior of the head valve is white. The intermediate valves (Figs. 61-62) are rectangular and beaked; their central areas are longitudinally striate; their lateral areas are radially striate and have 5-6 radial rows of eye spots. The sutural plates are connected to each other by a pectinate sinus plate; the insertion plate has 1 lateral slit which is deeply incised. The lateral side of the sutural plates and the lateral tooth are pectinate. The interiors of the intermediate valves are white and have chocolate-colored "V" patterns on their posterior regions. The 2nd valve is longer than the 3rd to 7th valves. The anal valve (Figs. 63-64) is flat and triangular in shape; its central area is longitudinally striate, its posterior area is hardly seen; the mucro is posterior and terminal. The sutural plates are large and are connected by a pectinated sinus plate. Neither insertion plate nor slit are present. In the place of the insertion plate there is a crescentic ridge. The interior of the anal valve is white.

The girdle, tessellated with white and chocolate-colored bands, is covered with extremely minute spicules (Fig. 65) on the dorsal side and square scales (Fig. 66) on the ventral side. On each side are 47 ctenidia, located in that part of the pallial groove corresponding to the dorsal location of the 2nd to 8th valves. Lappets of the pallial fold are present.

Radula (Fig. 67): The central tooth has a pestle-like base and a bidentate cusp. The central lateral tooth has a triangular base, with a slender cusp projecting from the base. The major lateral tooth has a basin-like cusp and its shaft has a medial projection. The major uncinus tooth has a leaf-like blade which is connected to a small base by a stalk.

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BRIEF COMMUNICATIONS

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THE CHROMOSOME NUMBER OF *BULINUS SERICINUS* FROM ETHIOPIA.[1][2] — The first case of polyploidy (tetraploidy) in pulmonate mollusks was found in a North American species of the planorbid genus *Gyraulus* (Burch, 1960a). This was followed by the observation that specimens of *Bulinus truncatus truncatus* (also belonging to the family Planorbidae) from the Sudan were tetraploid (Burch, 1960b), a discovery which initiated an intensive investigation of the chromosomes of the medically important genus *Bulinus*. Specimens of *B. t. truncatus* from Iran, Iraq, Egypt and Sardinia were subsequently found also to be tetraploid, as were specimens of *B. t. rohlfsi* from Ghana and *B. coulboisi* from Tanzania (Burch, 1964). Additional reports of tetraploidy in *Bulinus* followed: Natarajan, Burch & Gismann (1965) for West Aden (*"B. sericinus"*), Burch (1967a) and Brown & Burch 1967) for Ethiopia (*B.* sp.), and Burch & Lindsay (1970) for Corsica (*B. truncatus* ssp.), Mauritania (*B. truncatus rohlfsi*), and *B. guernei* (Gambia). Normal diploid populations were found to occur in Senegal, Liberia, Ghana, Angola, S. Africa, Rhodesia, Zambia, Tanzania, Kenya, W. Aden and Ethiopia (Burch, 1964, 1967a, b; Natarajan, Burch & Gismann, 1965; Brown, et al., 1967; Brown & Burch, 1967; Burch & Lindsay, 1970). The real cytological peculiarities of the genus *Bulinus* were not fully realized until the discovery that octoploidy occurred in a West Aden population (Burch, 1964). Octoploid populations were subsequently found to occur in Ethiopia (Burch, 1967a, b; Brown & Burch, 1967), and Burch (1967a) discovered a hexaploid population in Ethiopia.

The Ethiopian highlands seem to be especially significant for the *Bulinus* s.s. complex, because all 3 polyploid chromosome numbers (tetraploid: n=36; hexaploid: n=54; octoploid: n=72) known for the genus occur there (Burch, 1967a), as well as at least several morphologically distinct populations having the normal diploid (n=18) chromosome number (Burch, 1967b). The known distribution of these ploidy forms has been given by Brown & Burch (1967), and although these forms would appear to be distinct species (Burch & Huber, 1966), most of them appear to be without scientific names. Additionally, it is not known to which forms to apply the existing scientific names, because the chromosome numbers of the various nominal species are mostly not known. Of prime importance in this regard is to determine the chromosome number of *B. sericinus* (Jickeli, 1874), since that is the first valid scientific name to be applied specifically to *Bulinus* s.s. from the Ethiopian highlands. Before any real headway can be made in solving the taxonomic and nomenclatorial problems of *Bulinus* in Ethiopia, it is essential to determine accurately just what are the biological parameters of *B. sericinus*, and especially its place in the polyploid system mentioned above.

Because of the pertinence of determining the chromosome number of *B. sericinus*, I made 3 previous trips to its type locality (Toquor River at Merkerka, Eritrea) in 1965 and 1968 to obtain topotype specimens for cytological study. However, each time only a few specimens were found, and these did not survive air shipment to Ann Arbor. Field-preserved material obtained from these trips and investigated later in the laboratory, did not prove satisfactory for study, although on one occasion (the second trip in 1965), the chromosome number was determined (Burch, 1967a) for the nominal form *B. schackoi* (Jickeli, 1874)[3] from the Toquor River at Merkerka (the type locality of *B. schackoi* as well as *B. sericinus*.).[3] *B. schackoi* was found to be tetraploid, i.e., it had the chromosome number n=36.

In June 1969 I had the opportunity to visit Ethiopia for the 4th time, and to again collect snails in the Toquor River at Merkerka. This was during the dry season; the Toquor River was not flowing in the area collected, but consisted of numerous pools of standing water. Only 5 living specimens of *Bulinus* were found (none together, but each in a separate pool at a different part of the stream), although a species of each of the basommatophoran genera *Biomphalaria*, *Gyraulus*, *Radix* and *Ancylus* occurred in great abundance. Two of the specimens of *Bulinus* were low-spired and were distinctly and noticeably ribbed. These correspond to Jickeli's description of *B. sericinus*. The other 3 specimens were high-spired, of which 2 had nearly smooth shells, and the other high-spired specimen was ribbed. These 3 high-spired specimens correspond to Jickeli's *B. schackoi*.

The two live specimens with shells comparable to Jickeli's description of *Bulinus sericinus* were fixed several days after collection and slides were prepared[4] and studied in the Institute of Pathobiology, Haile Sellassie I University, Addis Ababa. These 2 specimens had 36 bivalents in male diakinesis and Metaphase I, and approximately 72 chromosomes in spermatogonial divisions (*exact* counts could not be made from the spermatogonial metaphase cells).

Bulinus sericinus is therefore a tetraploid species, like the nominal *B. schackoi*, and *B. truncatus* to the north and east and its subspecies *B. t. rohlfsi* in West Africa, and like *B. coulboisi* to the south (Tanzania). Other tetraploid populations of *Bulinus* in Ethiopia are known to occur in the Moggio River at Moggio (Burch, 1967a) and at 6 localities listed by Brown & Burch (1967): Northeastern shore of Lake Awasa at the entrance of the Black River, Sidamo Prov.: Bahar Dar town, Gojjam Prov.: 50 km northeast of Bahar Dar town on Gondar Rd., Begemedir Prov.: 37 km south of Gondar on Gorgora Rd., Begemedir Prov.: 1 km west of Aduwa road junction on Aksum Rd., Tigre Prov.: northwestern shore of Lake Zwai, Arussi Prov. Whether or not these other Ethiopian tetraploid populations all represent the species *B. sericinus*, or if some of them are actually *B. truncatus* or *B. coulboisi*, or yet another unnamed *Bulinus* species, is not known, and should be the subject of further studies.

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(2) Grateful acknowledgement is made to Dr. Aklilu Lemma for use of the facilities of the Institute of Pathobiology, Haile Sellassie I University, Addis Ababa, Ethiopia, and to C. M. Patterson for preparation of the slides.

(3) *Bulinus schackoi* differs from *B. sericinus* by being higher-spired, and it was originally described as larger. Mandahl-Barth (1958) considered the 2 species synonymous, which they may be, although Brown (1965) suggested that there may be at least some genetic difference between the 2 forms. I used the name *schackoi* in 1967a, because little was known about either of the 2 forms from this locality.

(4) The snail's shells were cracked near the apex, and the animals and shell were dropped into modified Carnoy's fixative (95% ethanol and glacial acetic acid, 3:1 parts by volume). Ten to 20 minutes later, the gonads were dissected out and used to make acetic-orcein squash preparations.

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NEW SPECIES OF TROPICAL EASTERN PACIFIC GASTROPODA[1][2] — In the course of assisting with the treatment of the Archaeogastropoda for the forthcoming revised edition of *Seashells of Tropical West America*, by Dr. Myra Keen, a number of new species have been recognized in the collections available to me. Descriptions of some of these have been published elsewhere (McLean, 1970a, 1970b, 1970c); in this paper descriptions of 17 additional archaeogastropods are given, along with 3 species of mesogastropods and 1 neogastropod.

Most notable of the new species is the 2nd tropical west American species of *Haliotis*. Two species of *Scissurella* (*Anatoma*) are included, a group previously unknown in the tropical eastern Pacific. New species of other generic taxa new to the region are in the subgenus *Clypidella* of *Fissurella* and the trochacean genus *Mirachelus* Woodring. Six species of *Tegula* (*Agathistoma*) are proposed as new. With these additions, this group of common intertidal species is represented by 16 tropical eastern Pacific species. Three species of *Arene* H. & A. Adams, and one *Macrarene* Hertlein & Strong, are included.

Type materials for 11 of the species were collected by the Allan Hancock Pacific Expeditions (1931-41) and are part of the Allan Hancock Foundation Collection, now on loan to the Los Angeles County Museum of Natural History. Two of the species were received from Andrê and Jacqueline DeRoy of Isla Santa Cruz, Galapagos Islands, Ecuador, one from Mr. Eugene Bergeron of Balboa, Canal Zone, one from Mr. Ray Maynard of Los Angeles, and one from Scripps Institution of Oceanography. The balance of the species were obtained by Los Angeles County Museum (LACM) field work. Three species were collected on separate expeditions to the Tres Marias Islands and to the Cape San Lucas area of Baja California on the R/V *Sea Quest*, in which Museum personnel were guests of Mr. and Mrs. Richard F. Dwyer of Corona del Mar, California.

Repositories for type materials described herein are as follows: AHF, Allan Hancock Foundation, University of Southern California (gastropod collection on loan to LACM); AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; SBM, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; SU, Stanford University, Paleontological Museum; USNM, United States National Museum of Natural History. The type lots of 11 of the species are represented in sufficient quantity to enable distribution of paratypes to each of the above institutions.

1. *Haliotis* (*Padollus*) *roberti* new species (Figs. 1-2)

Description of Holotype: Shell small, thin sculptured postnuclear whorls 2.5; apex low, situated at about the posterior 1/4 of the shell, holes 25, with 5 remaining open. Nucleus of one rapidly enlarging, smooth and rounded whorl, tip small. Early postnuclear sculpture gradually emerging, consisting of fine, slightly undulating spiral threads. On the penultimate whorl directly above the edge of the lip there are approximately 12 spiral cords between the preceeding suture and the row of holes, with a slightly stronger cord adjacent to the suture; below the row of holes there are 5 cords, becoming stronger and more broadly spaced near the succeeding suture. Along the edge of the lip, approximately 26 cords may be distinguished between the suture and the row of holes; cords are well elevated and rounded, with narrower interspaces; secondary cords emerge in the interspaces as the interspaces reach the width of the cords. The holes are weakly tubular, below are 5 minor cords and then 4 major cords with broad slopes in the direction of the columella. The area below the holes is only slightly concave. Axial sculpture consisting of undulating ridges radiating along the line of growth, 9 such ridges radiating out in the area of the shell that includes the last 7 holes. The radiating ridges are interrupted in a narrow band at about the mid-position on the whorl, although the spiral ribs remain strong through this area. Growth lines are minute and scarcely produce any sculptural effect, although some of the ribs may be cut into square beads. Pigmented outer edge of lip narrow, columella broad and smooth, extending internally for 2 whorls. External coloration pale orange with greenish-white flecking along the ribs; interior of similar hue with thin nacre reflecting pink and green. Length 18.6, width, 14.0, height, 6.8 mm.

Type Locality: Chatham Bay, Cocos Island, Costa Rica, 5° 33' 50" N, 86° 58' 55" W, 40-47 fathoms, R/V *Velero* station 780-38, 14 January 1938, 11 specimens (9 live-collected).

Type Material: Holotype, LACM-AHF 1368, 7 paratypes, LACM-AHF 1369, single paratypes, AMNH, CAS, and USNM. Specimens in the type lot range from a minimum length of 9.6 mm to a maximum of 18.6 mm (holotype).

Discussion: *Haliotis roberti* belongs to a group of small, reddish shelled, offshore tropical American species represented by *H. pourtalesii* Dall, 1881, from off the Florida Keys (Foster, 1946) and Yucatan (Harry, 1966), *H. barbouri* Foster, 1946, from Brazil, and *H. dalli* Henderson, 1915,

previously known only from the Galapagos Islands, but reported here for the first time from Gorgona Island, Colombia (AHF 851-38, 10-20 fathoms, 2 specimens). Of these *H. roberti* resembles the 2 Caribbean species more so than *H. dalli*. *Haliotis dalli* has a distinct channel below the row of holes and also has an elevated spiral ridge at the mid-dorsal position on the shell, and has regular radial sculpture. *Haliotis roberti* has broader and thicker spiral ribbing than *H. pourtalesii*, in which the ribbing is narrow and broadly spaced, and it differs from *H. barbouri* chiefly in lacking the strong nodes of the latter species.

The addition of a 2nd tropical west American species of *Haliotis* is an unusual event and I am pleased to name it for Robert R. Talmadge of Eureka, California, an assiduous student of the Haliotidae.

FIGS. 1-2, *Haliotis* (*Padollus*) *roberti* sp. nov., holotype, X2. FIG. 3, *Scissurella* (*Anatoma*) *epicharis* sp. nov., holotype, X15. FIG. 4, *Scissurella* (*Anatoma*) *keenae* sp. nov., holotype, X15. FIGS. 5-6, *Fissurella* (*Clypidella*) *morrisoni* sp. nov., holotype, X3. FIGS. 7-8, *Fissurella* (*Cremides*) *deroyae* sp. nov., holotype, X2. FIG. 9, *Mirachelus galapagensis* sp. nov., holotype, X7. FIG. 10, *Mirachelus corbis* (Dall, 1889), holotype, USNM 95023, X7.

2. *Scissurella* (*Anatoma*) *epicharis* new species (Fig. 3)

Description of Holotype: Shell small for the genus (possibly immature), low spired, fragile, translucent white, 3 whorls. Selenizone at periphery, open about 1/5 the circumference, edges sharp, projecting, the open slit extremely narrow. Axial sculpture of fine, evenly spaced growth lines, curved protractively above the selenizone, straight or slightly retractive across the base; spiral sculpture of fine raised ridges of similar strength and spacing, producing a rhomboidal cancellate pattern on the upper part of the whorl, but with fine, even cancellate sculpture on the base. The suture is laid below the lower edge of the selenizone, creating a channel of the same width as the selenizone. Umbilicus narrow, deep, partially obscured by a slight reflection of the inner lip. Height, 1.3, diameter, 1.9 mm. The holotype has a growth scar on the penultimate whorl in advance of the aperture.

Type Locality: Cartago Bay, Isabela (Albemarle) Island, Galapagos Islands, Ecuador, 0° 35' S, 90° 57' W, 12 fathoms, R/V *Velero* III bottom sample station 481, 21 January 1938, 2 specimens.

Type Material: Holotype, LACM-AHF 1370, paratype, LACM-AHF 1371.

Discussion: This and the following species are the first known tropical eastern Pacific species of *Scissurella* (*Anatoma*). Eastern Pacific species of Scissurellidae were reviewed by McLean (1967). Of the Californian species, *S. epicharis* most resembles *S.* (*Anatoma*) *lyra* Berry, 1947, which is more compressed and has axial ridges on the upper half of the whorl that are stronger than the spiral ridges. *Scissurella epicharis* has fine, even sculpture. The name is taken from the Greek, graceful.

3. *Scissurella* (*Anatoma*) *keenae* new species (Fig. 4)

Description of Holotype: Shell small for the genus, fragile, globose, whorls rounded, suture descending on the later whorls, color opaque yellowish-white. Nucleus of 1.5 smooth, glossy, unsculptured whorls with deeply impressed sutures. Postnuclear whorls 3.5, the selenizone arising about 1/3 of a whorl beyond the first appearance of axial sculpture. The fine, evenly spaced axial ridges on the upper half of the whorl are curved protractively and remain stronger than the fine spiral ribs that become apparent on the final 2 whorls. Selenizone at periphery, open about 1/5 the circumference, edges sharp, slightly raised. On the base the axial and spiral sculpture are nearly equal in strength, but the spiral cords are more broadly spaced, producing rectangular cancellations in a radiating pattern. Umbilicus narrow, deep, partially obscured by a slight reflection of the inner lip. Aperture circular, peritreme nearly complete. Height, 2.0, diameter, 2.0 mm.

Type Locality: Off northwest side, Angel de la Guarda [Guardia] Island, Gulf of California, Mexico, 29° 32' N, 113° 38' W, 46 fathoms, R/V *Velero* III bottom sample station 2033, 20 March 1937, 8 specimens, 2 of which are mature.

Type Material: Holotype, LACM-AHF 1372, 6 paratypes, LACM-AHF 1373; 1 paratype, USNM.

Referred Material: Additional specimens are represented in AHF bottom sample stations from the Gulf of California as follows: 275, off Raza Island, 40 fathoms, 6 specimens; 2005, San Jaime Bank, west of Cape San Lucas, Baja California, 75 fathoms, 1 specimen; 2010, Inner Gorda Bank, off Cape San Lucas, 80 fathoms, 3 specimens.

Discussion: In proportions *Scissurella keenae* resembles the wide ranging north boreal species *S. crispata* Fleming, 1832, but reaches only about 1/3 the size of that species. The latter species is known to range south to Cedros Island, outer coast of Baja California, at depths of 500-1000 fathoms. *Scissurella keenae* is evidently a fairly common species on mud bottoms in the Gulf of California at depths of 40-100 fathoms. It is a pleasure to dedicate this species to Dr. Myra Keen.

4. *Fissurella* (*Clypidella*) *morrisoni* new species (Figs. 5-6)

Description of Holotype: Shell small for the subgenus, thin, markedly depressed, ends of shell slightly elevated. Fissure forward of center, its posterior termination at about the midpoint of the shell, length of fissure about 4 times the width; fissure tripartite, constricted at both ends, walls of fissure sloping inward when viewed exteriorly; length of shell 5.5 times length of fissure. Surface of shell nearly smooth, sculptured with extremely fine radial grooves and fine concentric growth lines, appearing finely beaded under magnification. The termination of the grooves project slightly at the margins. Color purplish-brown with white rays; interior yellowish-green, glossy, transmitting the external color pattern. Length, 13.2, width, 9.5, height, 2.6 mm.

Type Locality: Bahia Honda, Panama, 7° 44' 25" N, 81° 32' 45" W, intertidal in rocky area, R/V *Velero* III station 861-38, 1 March 1938, 1 specimen.

Type Material: Holotype, LACM-AHF 1374.

Referred Material: Three lots, single beachworn specimens USNM 588191, USNM 588476, USNM 587950, all from San José Island, Perlas Islands, Panama, collected by Dr. J. P. E. Morrison, March, July and August, 1944. The largest of these, USNM 587950, measures: length, 16.2, width, 11.1, height, 2.6 mm.

Discussion: *Fissurella morrisoni* is referable to the subgenus *Clypidella* Swainson, 1840, distinguished by its extremely depressed shell, raised ends and elongate fissure, and on these characters differs widely from the tropical eastern Pacific fissurellas in the subgenus *Cremides* H. & A. Adams, 1854. *Fissurella morrisoni* differs from the 2 known Caribbean species of *Clypidella*, *F. fascicularis* Lamarck, 1822, and *F. punctata* Fischer, 1857 (see Farfante, 1943, p 12), in having extremely fine ribbing, rather than the coarse ribbing of the 2 Caribbean species. The species is dedicated to Dr. Joseph P. E. Morrison of the Division of Mollusks, U.S. National Museum, who has been most helpful during my visits to that institution, and whose industrious collecting in 1944 produced sufficient specimens of this remarkable species to warrant its description.

5. *Fissurella (Cremides) deroyae* new species (Figs. 7-8)

Description of Holotype: Shell small for the subgenus, sturdy but thin, moderately elevated. Fissure just forward of center, oblong, tripartite, particularly when viewed from the interior, approximately 1/10 the length of the shell. Radial sculpture of low, irregular, rounded ribs of varying width, separated by shallow grooves. The broader ribs project only slightly at the margin, forming a weakly crenulated edge. Color purplish-red, irregularly rayed with white. Interior glossy, pale greenish-white, showing concentric markings of darker green and transmitting the external pattern of white rays: callus area weakly bordered with pink. Length, 15.3, width, 9.5, height, 5.3 mm.

Type Locality: Academy Bay, Santa Cruz Island, Galapagos Islands, Ecuador, 0° 45' S, 90° 20' W, on surf exposed rocks at low tide. The type lot of 15 specimens was collected by Jacqueline DeRoy, of Santa Cruz Island, October, 1967.

Type Material: Holotype, LACM 1375; 6 paratypes, LACM 1376. Single paratypes, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: Numerous additional specimens from Isabela, San Cristobal, Santa Cruz, and Santa Maria Islands, Galapagos Islands, have been received from Mrs. DeRoy or are represented in the Hancock Collection. It evidently occurs only at the Galapagos Islands.

Discussion: *Fissurella deroyae* is the smallest of the tropical Eastern Pacific species of *Fissurella* (*Cremides*). Its color pattern is consistently red-rayed and it is the only species in which the greenish interior transmits the external pattern. Another common species on the Galapagos Islands, *F. obscura* Sowerby, 1835, is larger, has prominent projecting ribs and an interior of dark, opaque green.

6. *Mirachelus galapagensis* new species (Figs. 9, 11)

Description of Holotype: Shell small, nacreous within, conical, imperforate, suture deeply impressed. Tip of nucleus small, immersed, smooth, glassy, of one whorl. First of the 5 postnuclear whorls with fine axial ridges. On the penultimate whorl there are 3 spiral cords, beaded on crossing the retractively slanted axial ribs and producing square cancellations. The uppermost cord is directly below the suture, the lowermost cord is the strongest and is close to a spiral cord defining the base and upon which the suture is laid. On the penultimate whorl the middle of the 3 cords is closer to the lowermost cord. In addition to the main basal cord, there are 4 other basal cords, thinner and more closely spaced toward the columella. Columella slightly inflated toward the base. Lip edge sharp, about 10 lirate denticles within. Height, 3.6, diameter, 2.9 mm.

Type Locality: Off Canal Bolivar, near Tagus Cove, Isabela Island, Galapagos Islands, Ecuador, 0° 16' S, 91° 22' W, 40-55 fathoms. The type lot, consisting of 12 specimens was dredged by Andre and Jacqueline DeRoy, 23 January 1968.

Type Material: Holotype, LACM 1377, 3 paratypes, LACM 1378. Single paratypes, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: Approximately 90 specimens, 50-100 fathoms, from the type locality, Tagus Cove, are in the Hancock Collection, from station 155-34 and from bottom sample stations 432 and 461. In addition there is one specimen from station 143-34, 100-150 fathoms, Wenman Island, Galapagos Islands, and 15 specimens from bottom sample station 329, Cocos Island, Costa Rica, 40-46 fathoms.

Discussion: This is the first Eastern Pacific record of the genus *Mirachelus* Woodring, 1928 (p 438) (type species, *Calliostoma corbis* Dall, 1889, off Havana, Cuba). Dall's species is larger, reaching a length of 4.8 mm, has a more strongly pronounced columellar fold and has a much more strongly projecting peripheral cord than does *M. galapagensis*. The holotype of *M. corbis* is illustrated for comparison in Fig. 10.

The radula of a paratype specimen of *M. galapagensis* is illustrated in Fig. 11. The rachidian tooth is broadly flanged and has a pointed central cusp and 3 lateral cusps, as is illustrated for the genus *Euchelus* Philippi, 1847 (see Theile, 1924, fig. 1), indicating that the genus is closely related to *Euchelus*, as has been supposed. As in *Euchelus* the lateral teeth number 3 and the marginals are numerous.

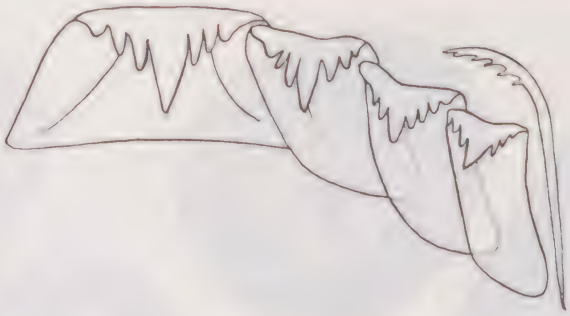

FIG. 11. *Mirachelus galapagensis* sp. nov., radula of paratype. Shown, left to right, the rachidian tooth, 3 lateral teeth, and the 1st marginal tooth. Greatly enlarged.

7. *Tegula* (*Agathistoma*) *bergeroni* new species (Figs. 12-13)

Description of Holotype: Shell of medium size for the subgenus, sculptured postnuclear whorls 5.5, suture moderately impressed, periphery and base angulate, base weakly convex, broadly umbilicate, columella with 3 denticles at base, aperture oblique, circular within. The suture is laid just below the cord defining the base; on the penultimate whorl the shoulder area is nodular below the preceding suture; midway across the whorl there is a strong nodular peripheral cord, between the subsutural cord and the peripheral cord are 3 weakly defined cords with broader interspaces; between the peripheral cord and the basal cord are 3 more cords. Fine spiral striae may be observed under magnification throughout. Base with about 7 broadly spaced, low cords. Early whorls mottled with grayish-brown, later whorls predominately yellowish-tan with brown stripes radiating from the suture, terminating on the outer lip and on the basal lip nearly perpendicular to the lip edge. Columella and a broad area adjacent to the umbilicus white; umbilical wall and the callus tongue weakly tinted with green. Height, 13.4, diameter, 14.4 mm.

Type Locality: Cabita Bay, near Cabo Corrientes, Colombia, 5° 29' 20" N, 77° 29' 35" W, intertidal, R/V *Velero* III station 229-34, 13 February 1934, 3 specimens.

Type Material: Holotype, LACM-AHF 1379; 1 paratype, LACM-AHF 1380; 1 paratype, USNM.

Referred Material: LACM 65-25, Taboga Island, Panama, 5-15 fathoms, 3 specimens; LACM B.368, Isla Senora, Perlas Islands, Panama, 8 specimens; AHF 239-34 and 859-38, Port Utria, Colombia, single specimens.

Discussion: *Tegula bergeroni* has the proportions only of *T. ligulata mariamadre* Pilsbry & Lowe, 1932, which is not known south of Manzanillo, Mexico. It differs from the latter species in its smaller size and different color pattern. *Tegula ligulata mariamadre* never has green in the umbilical area. Most species of *Tegula* (*Agathistoma*) exhibiting the green callus tongue invariably show it, but some specimens of *T. bergeroni* do not, in others a trace of green may be discerned deep within the umbilical cavity. The species is named for Eugene Bergeron of Balboa, Canal Zone, Panama, collector of numerous examples of this species and donor to the Museum's collections.

8. *Tegula* (*Agathistoma*) *corteziana* new species (Figs. 14-15)

Description of Holotype: Shell small for the subgenus, sculptured postnuclear whorls 4.5, suture impressed, periphery rounded, base convex, narrowly umbilicate, columella with one denticle at base, aperture oblique, circular within. Early whorls have 3 even spiral cords with broad interspaces; secondary cords arise in the interspaces, resulting in 5 developed cords on the penultimate whorl; along the outer lip a total of 16 developed cords between the suture and umbilicus; the interspaces are microscopically striate throughout. Color gray-brown, the cords mottled with lighter gray. Callus tongue bright green, the umbilical wall white, but bordered below with green; the green extending across the base of the columellar denticle and along the outer lip in a line marking the junction with the outer pigmented layer of the shell. Height, 10.5, diameter, 12.4 mm.

Type Locality: South side of Cabo Tepoca, Sonora, Mexico, 30° 16' N, 112° 30' W, mid intertidal. The type lot, consisting of 86 mature and 10 juvenile specimens, was collected by James H. McLean, LACM station 67-19, 26 March 1967.

Type Material: Holotype, LACM 1381; 71 paratypes, LACM 1382. Three paratypes each, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

FIGS. 12-13, *Tegula* (*Agathistoma*) *bergeroni* sp. nov., holotype, X3. FIGS. 14-15, *Tegula* (*Agathistoma*) *corteziana* sp. nov., holotype, X3. FIGS. 16-17, *Tegula* (*Agathistoma*) *felipensis* sp. nov., holotype, X2. FIGS. 18-19, *Tegula* (*Agathistoma*) *picta* sp. nov., holotype, X2. FIGS. 20-21, *Tegula* (*Agathistoma*) *verdispira* sp. nov., holotype, X3. FIGS. 22-23, *Tegula* (*Agathistoma*) *verrucosa* sp. nov., holotype, X2.

Referred Material: Numerous lots of this species are in museum collections, including 35 lots in the LACM collection. The species is found at every rocky intertidal locality from the head of the Gulf of California, south to at least Guaymas, Sonora, on the east and to Ceralvo Island on the western side of the Gulf. It is not known from the vicinity of Cape San Lucas.

Discussion: This abundant Gulf of California species has been confused chiefly with *Tegula globulus* (Carpenter, 1857). A specimen of *T. corteziana* was illustrated as *T. globulus* by Keen, 1958 (p 258, fig. 52). The lectotype of *T. globulus* was illustrated by Keen, 1968 (p 403, pl. 57, figs. 52a-b). *Tegula globulus* is a smaller species with more numerous spiral cords on the early whorls, has a more glossy surface and a broader range of color patterns. It occurs from Mazatlan to Acapulco. Distributions of the 2 species are not known to overlap, although the occurrence of either species between Guaymas and Mazatlan is unknown for lack of collections from this area. *Tegula corteziana* is a characteristic Gulf of California species, and the name is derived from another name for the Gulf, the Sea of Cortez.

9. *Tegula* (*Agathistoma*) *felipensis* new species (Figs. 16-17)

Description of Holotype: Shell of medium size for the subgenus, whorls 5 (excluding nucleus), suture moderately impressed; midway on the whorl there is an angulation, but the base is rounded; base slightly convex, broadly umbilicate, columella with 3 denticles at base, aperture oblique, circular within. On the penultimate whorl the shoulder area below the preceding suture is flat and bears 4 major spiral cords of irregular strength and spacing; the peripheral cord is thick and projecting, between it and the suture below are 4 irregular major cords, with irregular fine spiral striae throughout. Base with about 11 spiral cords of irregular strength and spacing; the cords are rounded and have narrower interspaces; directly in advance of the aperture the basal cords are worn smooth. Ground color yellowish-green with axial markings of brown that tend to run parallel to the advancing lip. Base of columella and callus tongue bright green. Height, 15.4, diameter, 17.2 mm.

Type Locality: Punta San Felipe, Baja California del Norte, 31° 02' N, 114° 49' W, among small rocks, low tide. The type lot, consisting of 19 mature and 14 juvenile specimens, was collected by James H. McLean, April, 1961, and December, 1962.

Type Material: Holotype, LACM 1383; 16 paratypes, LACM 1384. One mature and one juvenile paratype each, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: Abundant material of this species is represented in collections from San Felipe. It is uncommon at Puertecitos [Puertocitos], Baja California (SBM 06939); and at Punta Peñasco, Sonora (SBM 15905).

Discussion: *Tegula felipensis* has generally been identified as *T. mariana* Dall, 1919, but differs from that species in having stronger spiral cording and a dull, rather than shiny surface. The basal cords of *T. mariana* are low, narrow, and broadly spaced, while those of *T. felipensis* are coarse and rounded, with narrower interspaces. Large specimens of *T. mariana* may show a concavity in the subsutural area and coarse nodulations on the peripheral cord, features not shown in *T. felipensis*. San Felipe is the center of abundance of this species; it is rare at Punta Peñasco to the west and at Puertecitos [Puertocitos] to the south. *Tegula mariana* is unknown from San Felipe but is abundant both at Punta Peñasco and Puertocitos. At San Felipe the substrate is fine silt or clay and the water is seldom clear, giving rise to peculiar ecological conditions and no doubt favoring the localized distribution of some species, while excluding others.

10. *Tegula* (*Agathistoma*) *picta* new species (Figs. 18-19)

Description of Holotype: Shell large for the subgenus, 6 whorls, weakly convex, suture not impressed, base angulate, nearly flat, narrowly umbilicate, 3 denticles at base of columella, aperture oblique, lirate within. Spiral sculpture of nodular cords, with slightly broader interspaces, 4 cords on 3rd whorl, 6 on penultimate whorl, counting the broad, weakly defined subsutural cord, but not the strongly projecting cord defining the base. Base nearly flat, surface glossy, with 7 narrow, low cords, broadly spaced but more closely spaced toward the umbilicus. Body whorl with fine spiral striae, but on the base the striae are broadly spaced and faint. Axial sculpture of fine growth lines. Color greenish-white with broad axial stripes of pinkish-tan, on the base the stripes are brown in the interspaces and bright pink on crossing the basal cords; base of columella and callus tongue bright green. Height 18.5, diameter, 20.2 mm.

Type Locality: West of Manta, Ecuador, 0° 56' 43" S, 80° 44' 43" W, on exposed reef at low tide, R/V *Velero* III station 403-35, 20 January 1935, 23 specimens.

Type Material: Holotype, LACM-AHF 1385; 14 paratypes, LACM-AHF 1386. Single paratypes, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: Eleven lots from Ecuador and Peru are in the LACM collection, the northern extreme at Cape San Francisco, Ecuador (AHF 848-38), the southern, Talara, Peru (A.7408).

Discussion: *Tegula picta* has no doubt been regarded as the same as *T. verrucosa* sp. nov. (*T. byroniana* of authors), but differs in having 1/3 to 1/2 as many pustules on the spiral cords, in having a glossy base with low, narrow cords rather than the coarse cords of *T. verrucosa*, and in having pinkish-tan rather than purplish-brown coloration. The 2 species are evidently closely related, but no intergradation has been observed. *Tegula picta* has a more restricted, more southern distribution. The name is taken from the Latin, "painted," and describes the bright pattern of coloration, the name taken from a manuscript label of W. H. Dall in the U.S. National Museum.

11. *Tegula* (*Agathistoma*) *verdispira* new species (Figs. 20-21)

Description of Holotype: Shell small for the subgenus, sculptured postnuclear whorls 5, suture impressed, periphery rounded, base weakly angulate, broadly umbilicate, columella with 1 prominent denticle at the termination of the bright green, flat cord bordering the umbilicus, another sharp denticle just below; aperture oblique, circular within, lip lirate within. Penultimate whorl with 7 narrow, sharp spiral cords, interspaces broader than the cords, not spirally striate. Base with 8 narrow cords, with broader interspaces, cords more broadly spaced toward the umbilicus. Spiral sculpture of fine growth lines, produced into fine microscopic lamellae just below the suture and on the interspaces between basal cords, particularly those close to the umbilicus. Color, mottled brown, tan and white, with alternating light and dark areas on the spiral cords of the body whorl and base. The broad spiral platform descending into the umbilicus is bright green, the umbilical wall smooth and white, the callus tongue is unusually narrow and is bright green. Height, 9.0, diameter, 11.8 mm.

Type Locality: South anchorage, Maria Magdalena Island, Tres Marias Islands, Mexico, 21° 35' N 106° 35' W, in rocky area at low tide. The type lot, consisting of one mature and one juvenile specimen, was collected by James H. McLean, LACM station 65-11, 15 March 1965, from the R/V *Sea Quest*.

Type Material: Holotype, LACM 1387; paratype, LACM 1388.

Referred Material: CAS 24108, Maria Magdalena Island, 4 specimens; CAS 23779, Maria Magdalena Island, 5-10 fathoms, 1 specimen; SDNHM 40044, Tres Marias Islands, 2 specimens; ANSP 142731, Maria Magdalena Island, 3 specimens; LACM A.3991, Los Frailes, Baja California, 1 specimen.

Discussion: *Tegula verdispira* is the only Eastern Pacific species having the spiral platform descending into the umbilicus. The same structure is found in the Caribbean species *T. lividomaculata* (C. B. Adams, 1845), but that is a much larger species lacking the green coloration in the umbilical area. Most of the known specimens of *T. verdispira* were mixed with lots of *T. globulus*, a smaller, more elevated species with weaker spiral cording. The single specimen from Los Frailes, Baja California, was mixed with specimens of *T. corteziana* sp. nov., from which *T. verdispira* is readily distinguished in lacking the pronounced spiral striae in the interspaces of the spiral cords. My own collecting at Los Frailes and nearby Pulmo Reef has yielded neither of the 2 new species, however. Another related species is the Caribbean *T. maculostriata* (C. B. Adams, 1845), which is known in the eastern Pacific only at Cocos Island, Costa Rica, where it was first reported by Pilsbry & Vanatta (1902, p 559). Although broadly umbilicate, it does not have an umbilical platform or groove, and has smoother spiral cords than *T. verdispira*. The name, meaning green spiral, directs attention to the most characteristic feature of this species.

12. *Tegula* (*Agathistoma*) *verrucosa* new species (Figs. 22-23)

Description of Holotype: Shell large for the subgenus, 6 whorls, weakly convex, suture not impressed, base angulate, nearly flat, narrowly umbilicate, 3 denticles at base of columella, aperture oblique, lirate within. Spiral sculpture of nodular cords, with equal interspaces, the nodes closely spaced, 4 cords on 3rd whorl, 6 on penultimate whorl, counting the broad weakly defined subsutural cord, but not the strongly projecting cord defining the base. Interspaces with about 5 sharply cut spiral striae between cords; base nearly flat, with 8 strong, rounded cords with nearly equal interspaces, interspaces with about 3 sharply raised spiral striations between cords. Axial sculpture of fine growth lines. Color predominantly dark reddish-brown, with axial markings of dark yellow-green; base brownish with interrupted lighter markings along the spiral cords. Base of columella and callus tongue green. Height, 19.6, diameter, 21.7 mm.

Type Locality: Palo Seco, Canal Zone, Panama, 8° 55' N, 79° 34' W, rocky intertidal. The type lot, consisting of 14 specimens, was collected by Eugene Bergeron in 1963.

Type Material: Holotype, LACM 1389, 5 paratypes, LACM 1390. Single paratypes, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: Seventeen lots of this species are represented in the LACM and AHF collections, ranging from La Libertad, El Salvador, to Panama. The only lot examined from south of Panama is CAS 36663, from Sechura Bay, Peru.

Discussion: This is *Trochus reticulatus* Wood, 1828 (not Sowerby, 1821): *Tegula byroniana* of authors, not Wood, 1828. Type material of *Trochus byronianus* Wood, 1828, originally said to be from the "Sandwich Islands" [Hawaii], has been examined and photographed in the British Museum by Dr. Myra Keen. I concur with Dr. E. Alison Kay (1966, p 2), that *T. byroniana* represents the south Caribbean species *T. viridula* (Gmelin, 1791), which differs from both *T. verrucosa* and *T. picta* sp. nov. in having a more impressed suture and a rounded rather than angulate base. This familiar Panama species is consequently without a name, and *T. verrucosa*, from the Latin, "full of warts," with reference to the nodulose sculpture on the spiral ribs, is proposed.

13. *Arene adusta* new species (Figs. 24-25)

Description of Holotype: Shell of medium size for the genus, solid, umbilicate, nacreous within, suture deeply channeled, whorls rounded, base angulate, nearly flat. Nucleus of 1.5 flattened, singly carinate whorls: postnuclear whorls 3.5. Spiral sculpture on early whorls of 4 beaded cords that gradually take shape on emerging from the nucleus. On the body whorl are 4 beaded cords of nearly equal size, interspaces equal. The suture is laid upon a broader and more projecting basal cord until the final half whorl, when this cord is exposed by the descending suture. Base with 6 prominent beaded cords, one bordering the umbilicus and another descending within. Axial sculpture of fine lamellae over entire surface, beading on the spiral cords produced by the thickening and overlapping of 5-8 layers of lamellae in the direction of growth. Lip greatly thickened, spiral cords of base reflected outward and then inward, when seen in basal view. Color tan, with darker and lighter areas upon the spiral cords in a radial pattern, area adjacent to umbilicus lighter colored. Height, 4.8, diameter, 6.1 mm.

Type Locality: Cove adjoining the west sides of Isla Partida and Espiritu Santo Islands, Baja California, Mexico, 24° 25' N, 110° 25' W, LACM station 66-28, 10 April 1966. The type lot, consisting of 29 hermit crab specimens was collected by James H. McLean and Peter M. Oringer by skin diving at approximately the low water line, from the R/V *Sea Quest*.

Type Material: Holotype, LACM 1391: 20 paratypes, LACM 1392. Single paratypes, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: USNM 558435, Isla Partida, Baja California, one specimen with operculum in place, collected by Hawkins.

Discussion: *Arene adusta* is closely related to *A. lurida* Dall, 1913, but differs chiefly in having an angulate base rather than the evenly rounded base of *A. lurida*. Differences between immature shells of the 2 species are even more pronounced, the juvenile shells of *A. adusta* are discoidal in shape, while those of *A. lurida* are rounded. Approximately 50 specimens of *A. lurida* were collected with the type lot of *A. adusta*. Nearly all were living: they are somewhat smaller and colored gray or brick red, rather than tan as in *A. adusta*. *Arene lurida* has been collected at many of the islands along the southwestern shore of the Gulf of California, while *A. adusta* is known only from the vicinity of Espiritu Santo Island. The name is a Latin adjective, "brown" or "tanned."

14. *Arene ferruginosa* new species (Figs. 26-29)

Description of Holotype: Shell of medium to large size for the genus, sturdy but not massive, umbilicate, nacreous within, suture deeply channeled, whorls and base rounded. Nucleus of 1.5 flattened whorls with a single carination, 4 postnuclear whorls. Spiral sculpture on early whorls of 3 cords, the uppermost consisting of a row of projecting, rounded beads, the other 2 unbeaded until reaching the final whorl and a half. Weak, beaded interstitial cords emerge next to the upper 2 of the original 3 cords on the final whorl. The suture is laid on a strong cord that delimits the base, but does not strongly project. The basal cord is exposed by a slightly descending suture on the final whorl. Base sculptured with 6 major and 1 minor cord, 1 bordering the umbilicus and 2 descending deep within. Axial sculpture of fine growth lamellae over entire surface, apparent chiefly in the interspaces between cords but not directly on the beaded surfaces. Lip not thickened, growing edge sharp. Color brick red, with scattered white flecking along the spiral cords. Height, 6.0, diameter, 6.9 mm.

Type Locality: South of White Friars, Mexico, 17° 30' 50" N, 101° 29' 55" W, 25 fathoms on rocky bottom, R/V *Velero* III station 264-34, 2 March 1934, 1 specimen.

Type Material: Holotype: LACM-AHF 1393.

Referred Material: Specimens are represented from the following AHF bottom sample stations: 332, Bahia Honda, Panama, 30-50 fathoms, 34 specimens, mostly fragmentary and in subfossil condition; 330, Chatham Bay, Cocos Island, Costa Rica, 47 fathoms, 2 specimens; 430, Wenman Island, Galapagos Islands, Ecuador, 150 fathoms, 3 specimens.

Discussion: *Arene ferruginosa* differs from all Eastern Pacific and Western Atlantic species known to me in having only the uppermost cord beaded on the early whorls. Of the 11 eastern Pacific species

it is the only one characteristically found in moderately deep water: the other species occur at depths of 20 fathoms or less. It is one of the few species of *Arene* not having a greatly thickened mature lip. In this feature it is similar to *A. bairdii* (Dall, 1889), a brick red Caribbean species occurring at similar depths. The latter species does not show the peculiar beading feature of the early ribs of *A. ferruginosa*. The specimens from Wenman Island, Galapagos Islands (Figs. 28-29), and Cocos Island, Costa Rica, reach only 3 mm in height but are evidently mature because the suture descends on the final whorl. Dwarf populations apparently occur at these localities. The name means rust-colored, with reference to the brick red coloration.

15. *Arene stellata* new species (Figs. 30-31)

Description of Holotype: Shell small to medium sized for the genus, solid, low spired, broadly umbilicate, nacreous within, suture deeply channeled: periphery with 2 strongly projecting spinose carinations. Nucleus of 1.5 flattened, singly carinate whorls: postnuclear whorls 3.5. Spiral sculpture on early postnuclear whorls consisting of a row of beads close to the suture and a projecting peripheral cord bearing fluted scales: on the final whorl below the suture there is first a broad horizontal shelf, followed by a prominent row of beads, then a slightly convex area sloping down and bearing 3 weak rows of beads, then a smooth concave area leading to the projecting peripheral keel, which

FIGS. 24-25, *Arene adusta*, sp. nov., holotype, X6. FIGS. 26-27, *Arene ferruginosa*, sp. nov., holotype, X5. FIGS. 28-29, *Arene ferruginosa*, AHF 430, Wenman Island, Galapagos Islands, X8. FIGS. 30-31, *Arene stellata* sp. nov., holotype, X7. FIGS. 32-33, *Macrarene lepidotera* sp. nov., holotype, X4.

bears regularly spaced fluted scales. Area between the 2 projecting carinations deeply cut, with a smooth vertical wall; the basal carination projects less strongly than the upper carination and bears more numerous fluted scales (3 in the same space for 2 on the upper carination). Base weakly convex, bearing 3 rows of fine beads away from the edge. Umbilicus broad, and bearing 3 coarsely beaded cords separated by nearly equal interspaces. Axial sculpture over the entire surface of fine raised lamellae. Peritreme complete (umbilical wall broken in holotype). Height, 2.9, diameter, 4.8 mm.

A paratype specimen 4.8 mm in diameter lacks the upper 1/2 of the shell but has a mature lip, showing that the suture descends on the last 1/5 turn, that the mature lip is slightly thickened, and that 4.8 mm in diameter is approximately the mature size.

Type Locality: Cove adjoining the west sides of Isla Partida and Espiritu Santo Islands, Baja California, Mexico, 24° 25' N, 110° 25' W, LACM station 67-27, 10 April 1966. The type lot, consisting of 5 fragmentary or immature dead specimens was collected by diving on rocky bottom at 20-30 feet by James H. McLean, from the R/V *Sea Quest*.

Type Material: Holotype, LACM 1394; 4 paratypes, LACM 1395.

Referred Material: SU 50999, 3 nepionic specimens, 14-25 fathoms, Espiritu Santo Island, Belvedere Expedition, 1960.

Discussion: *Arene stellata* is the only low spired species with a stellate periphery known in the eastern Pacific. It is related to a group of similar Caribbean species, the best known of which is *A. cruentata* (Mühlfeld, 1829), the type species of *Arene* Adams & Adams, 1854. *Arene stellata* is smaller, lacks the red markings and has 2, rather than the 3 peripheral carinations of *A. cruentata*. Subgeneric separation of this group from those related to the other 2 species described above does not seem to be warranted, because there are Caribbean species not definitely assignable to either group.

16. *Macrarene lepidotera* new species (Figs. 32-33)

Description of Holotype: Shell of medium size for the genus, sturdy, yellowish-white, low spired, broadly umbilicate, nacreous within, suture deeply channeled, peritreme complete. Nucleus of 2 smooth, rounded nuclear whorls in a plane coil, postnuclear whorls 3.5, the suture descending slightly on the final whorl. Early postnuclear whorls with thin axial ridges running suture to suture; after one whorl 3 spiral carinations emerge, one on the shoulder, a more prominent one at the periphery and one barely left exposed by the following suture. Axial sculpture of fine overlapping lamellae throughout and of narrow raised axial ridges, 16 on the final and penultimate whorls, elevated on crossing the shoulder cord and forming strong fluted scales on crossing the main peripheral cord. Spiral sculpture on base consisting of a strong cord bordering the umbilicus, another less pronounced cord midway on the umbilical wall, and, between the main basal cord and the major peripheral carination, 4 separate cords, the 2 closest to the umbilicus more closely spaced, the outer 2 bearing fluted scales, these scales numbering 4-6 between major axial ribs. Aperture entire, lip not greatly thickened, but the 3 preceding axial ribs are thicker and more closely spaced than earlier ribs. Height, 7.1, diameter, 10.0 mm.

Type Locality: Off Braithwaite Bay, Socorro Island, Revillagigedo Islands, Mexico, 18° 40' 42" N, 110° 55' 58" W, 70-75 fathoms on rocky bottom, R/V *Velero* III station 925-39, 18 March 1939, 1 specimen.

Type Material: Holotype, LACM-AHF 1396.

Referred Material: All Revillagigedo Islands, Mexico: LACM A.375, Clarion Island, 40 fathoms, 1 specimen, George Willett; AHF 137-34, Clarion Island, 57 fathoms, 1 immature specimen; USGS (Geological Survey, Menlo Park, Calif.) sta. SU-91-67, San Benedicto Island, 128-130 fathoms, 10 specimens (9 immature), in subfossil condition.

Discussion: *Macrarene lepidotera* is closely related to *M. farallonensis* (A. G. Smith, 1952), a species described from off the Farallon Islands, California, but represented in the AHF collections from as far south as Cape San Lucas, Baja California. *Macrarene lepidotera* differs from *M. farallonensis* in having 4 scaly cords rather than a single smooth spiral cord between the stellate periphery and the main basal cord. Specimens also tend to be smaller and to have more numerous axial ribs. The name is a Greek adjective, derived from the noun *lepidion*, "little scale," with reference to the characteristic scaly sculpture of the basal cords.

17. *Tricolia diantha* new species (Figs. 34-35)

Description of Holotype: Shell small for the genus, postnuclear whorls 3.5. Nucleus of one flattened whorl, 1st postnuclear whorl developing a single angular carination that lasts only 2/3 of one turn. Later whorls rounded, suture descending on final whorl, the immediate subsutural area on the final whorl flat or slightly concave. Later whorls sculptured with fine, even spiral striae, approximately 15 striations exposed on the penultimate whorl above the termination of the lip, 6 on the whorl directly

above. Aperture proportionately large, nearly circular, outer lip thin, inner lip bordering a narrow umbilical chink; in basal view, the extremely narrow umbilicus is partially obscured by the inner lip. Color whitish-pink, with wavy and sometimes interrupted axial striping of darker pink, a slight whitish blotching on the back side of the last whorl. Height, 2.1, diameter, 1.7 mm.

Type Locality: East of south end, Albemarle (Isabela) Island, Galapagos Islands, Ecuador, 0° 55' S, 90° 30' W, 60 fathoms, R/V *Velero* III bottom sample station 450, 26 January 1934, 54 specimens, none live-collected.

Type Material: Holotype, LACM-AHF 1397; 37 paratypes, LACM-AHF 1398. Two paratypes each, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: AHF 193-34, Post Office Bay, Charles Island (Santa Maria), 8-10 fathoms, 2 specimens with operculum in place. Additional specimens are represented from AHF bottom sample stations 401, 402, 429, 430, 435 and 464, including San Cristobal, Santa Maria, and Wenman Islands, at depths ranging from 9 to 150 fathoms.

Discussion: *Tricolia diantha*, the only species of *Tricolia* known to occur at the Galapagos Islands, differs from all other eastern Pacific species in its color pattern of dark pink markings on a lighter pink ground, emphasized by the name, pink. The operculum (AHF 193-34) is calcarous, white, with microscopic striae running perpendicular to the outer edge. Although most of the type lot is consistently colored like the holotype, some of the lots show a predominance of pink spotting or broad white banding or mottling.

FIG. 34, *Tricolia diantha* sp. nov., holotype, X15. FIG. 35, *Tricolia diantha*, AHF 193-34, Post Office Bay, Galapagos Islands, X15. FIG. 36, *Littorina albicarinata* sp. nov., holotype, X6. FIG. 37, *Turritella parkeri* sp. nov., holotype, X1.5. FIG. 38, *Turritella parkeri*, detail of early whorls (AHF 237). FIG. 39, *Niso emersoni* sp. nov., holotype, X4. FIG. 40, *Niso emersoni*, paratype, X4. FIG. 41, *Nassarius shaskyi* sp. nov., holotype, X2.

18. *Littorina albicarinata* new species (Fig. 36)

Description of Holotype: Shell small for the genus, turbinate, spire elevated, nuclear whorls eroded; sculptured postnuclear whorls five. Spiral sculpture on penultimate and early whorls consisting of 2 thin, strongly projecting, rounded carinations. Above the upper carination the surface of the whorl slopes evenly toward the suture and bears 6 evenly spaced incised spiral lines; the face of the whorl between the 2 main carinations is nearly vertical and also has about 6 incised spiral lines. Base with 1 major and 3 minor cords and spirally incised lines. Axial sculpture wanting. Columellar area narrow, continuous with the basal lip, the callus on the parietal wall meeting the upper extremity of the lip; a weak umbilical groove outside the callus. Spiral carinations whitish, early whorls dark brown, body whorls grayish with brown maculations crossing the carinations, columella white, aperture dark brown. Height, 4.7, diameter, 3.2 mm.

Type Locality: El Requeson, Concepcion Bay, Baja California, 26° 38' N, 111° 50' W. The type lot, consisting of approximately 200 specimens, was collected in August 1963 by Ray Maynard. Specimens were picked from gravel collected by shallow diving. None of these specimens were live-collected, but this lot is selected because it includes a number of exceptionally large specimens.

Type Material: Holotype, LACM 1399, 50 paratypes, LACM 1400. Four paratypes each, AMNH, ANSP, CAS, MCZ, SBM, SU and USNM.

Referred Material: Numerous specimens of this species are represented in museum collections from stations ranging from the head of the Gulf of California, to at least as far south as Guaymas on the east, and to Rancho el Tule, near Cape San Lucas, Baja California, on the western side of the Gulf. Living specimens occur in crevices near barnacles in the mid-intertidal zone.

Discussion: Collectors in the Gulf of California have long been aware of this species. *Littorina albicarinata* is the smallest of the eastern Pacific littorines and is the only strongly carinate species. Variation is extensive. In some specimens the carinae are weakly developed or dark colored. The number and strength of the basal cords is also variable. Often occurring with the new species is a species of *Fossarus*, cf. *F. atratus* (C. B. Adams, 1852), of similar size and markings, which differs in having a lower spire, broader umbilical chink, and less pronounced carinations.

A more detailed examination of the relationships among the eastern Pacific littorines and *Fossarus* is desirable. The new species is tentatively referred to *Littorina* in the broad sense until such work is done. The name means white-keeled, referring to the characteristic feature of this species.

19. *Turritella parkeri* new species (Figs. 37-38)

Description of Holotype: Shell of medium size, nucleus lost, remaining whorls 14, surface chalky and eroded near apex, near the aperture there are thin periostracal remnants. Earliest whorls with a single projecting carination at 1/3 the distance from the anterior suture, persisting on later whorls as the single strong carination at 1/4 the distance above the suture, the area below beveled in toward the suture. On the penultimate whorl there are in addition 4 weakly defined spiral cords and fine irregular spiral striae throughout. The base is defined by an angularity, just below which the suture is laid, producing a deeply indented suture. Base nearly flat, with fine, scarcely perceptible spiral striae. Growth line trace producing a broad sinus, in nearly central position on the whorl. Aperture rounded quadrate, lip and columella thin, parietal area glossy. Color tan, with irregular dark markings along the growth line trace. Height, 48.4, diameter, 13.4 mm.

Type Locality: West of Espirutu Santo Island in Bahia de La Paz, Baja California, 24° 24.3' to 24° 25.6' N, 110° 23.7' to 110° 25.5' W, 45-65 fathoms, R/V *Thomas Washington* (Scripps Institution of Oceanography) station MV 68-I-29, 12 January 1968, 74 specimens, 15 in fresh condition.

Type Material: Holotype, LACM 1401, 27 paratypes, LACM 1402; 30 paratypes, Scripps Collection. Two paratypes each, AMNH, ANSP, CAS, MCZ, SBM, SDNHM, SU and USNM.

Referred Material: AHF bottom sample station 247, 3 miles off San Gabriel Bay, Espiritu Santo Island, 80 fathoms, 3 specimens (Fig. 38); Shasky Collection (Redlands, California), off east side, Espiritu Santo Island, 40-90 fathoms, Ariel Expedition, 1960, 4 specimens.

Discussion: *Turritella parkeri* was illustrated by Parker (1964, pl. 7, fig. 1, "*Turritella* sp.") as a species characteristic of deep northern basins and troughs in the Gulf of California, 230-1400 meters in depth, but I am unable to determine the station of his specimen. It is, however, a species found at greater depths than other eastern Pacific *Turritella*. It is evidently related to *T. cooperi* Carpenter, 1864, and *T. mariana* Dall, 1908, 2 eastern Pacific species in which the single prominent carination near the base of the early whorls persists in the same position on the adult whorls. *Turritella parkeri* is broader than both of these species and bears a single prominent carination on mature whorls, while both *T. cooperi* and *T. mariana* develop 2 or more strong carinations per whorl. The early sculpture of *T. parkeri* is illustrated in Fig. 38. The largest of the LACM paratypes measures 57 mm in length (nuclear whorls lost), 16 mm in diameter. *Turritella parkeri* is named for Robert H. Parker, whose 1964 paper is an important source of ecological data for many Eastern Pacific species.

20. *Niso emersoni* new species (Figs. 39-40)

Description of Holotype: Shell of medium size for the genus, surface highly polished, narrowly but distinctly umbilicate. Nuclear whorls 3.5, slightly convex, nuclear whorls and 1st postnuclear whorl dark reddish-brown, followed by 3 whitish, flat-sided whorls. Postnuclear whorls 12, body whorls colored reddish-brown, color increasing in intensity in direction of growth for 1/8 to 1/3 of a whorl, color then abruptly dropping to a lower intensity and increasing in the direction of growth. On the final whorl a fine raised but rounded ridge defines the periphery, ridge of slightly darker intensity of the color above: below the peripheral ridge the basal area has a broad white band of 1/3 the basal width: the remaining 2/3 of the basal area, including the umbilical ridge, is dark brown: umbilical wall and inner lip opaque white. The subperipheral band of white is reflected on the inner side of the outer lip. Early whorls nearly flat-sided, suture not impressed: penultimate and final whorl slightly convex, suture slightly channeled. Outer lip thin, inner lip curved and revolute. Height, 12.2, diameter, 4.1 mm.

Type Locality: Off San José Point, Guatemala, 13° 52' 30" N, 91° 10' 30" W, 7-11 fathoms on black sand, R/V *Velero* III station 770-38, 11 January 1938, 4 specimens.

Type Material: Holotype, LACM-AHF 1403, 1 paratype, LACM-AHF 1404, 1 paratype, USNM, 1 paratype, AMNH. Each of the 3 paratypes have 1 or 2 holes bored by naticids, but all have complete apertures and complete nuclear whorls. The largest paratype measures 15.5 mm in height. One of the specimens is predominantly white (Fig. 40), but the nuclear whorls are the same reddish color in all the specimens.

Referred Material: Shasky Collection (Redlands, California), one specimen from Chiapas, Mexico, 30 miles north of Guatemala border, by shrimp trawler, March, 1961.

Discussion: *Niso emersoni* is the only eastern Pacific species having dark early whorls; the body whorls are also more intensely colored than in other species. Its color pattern is similar to that of *N. interrupta* (Sowerby, 1834), but *N. emersoni* has a whitish subsutural band and lacks the dark color of the inner lip and umbilicus of *N. interrupta*. *Niso portoricencis* Dall & Simpson, 1901, is a Caribbean species with dark nuclear whorls, but the shell of that species is broader, with a whitish band just above the suture. The species is dedicated to Dr. William K. Emerson of the American Museum of Natural History, who recently reviewed the eastern Pacific species of *Niso* (Emerson, 1965).

21. *Nassarius shaskyi* new species (Fig. 41)

Description of Holotype: Shell relatively large, massive, nucleus of three smooth, polished, rounded whorls, tip immersed: postnuclear whorls seven, sutures distinct but not deeply impressed. Axial sculpture of ten ribs, rounded and extending from suture to suture, with broad interspaces on the first three whorls, nearly obsolete in the shoulder area and cresting at the midpoint on later whorls. On the final whorl the ribs crest even more strongly at the basal angularity, the rib surfaces slightly concave between the upper and lower crests, ribs extending across the base but becoming obsolete at the edge of the fossa. Spiral sculpture on the first sculptured whorl of six raised threads with nearly equal interspaces, overriding the axial ribs: on the fifth sculptured whorl the ribs have increased to about 13 and the interspaces or grooves are narrower: on the penultimate whorl the spiral ribs become weak and broadly spaced: on the final whorl the ribs are obsolete particularly in the area between the upper and lower axial crests, which are nearly smooth. Outer lip with a strong varix, lip edge rounded, lirate internally: inner lip producing a broad columellar shield, completely obscuring the body whorl, shield with irregular, undulating ridges and a strong ridge defining the anal notch: canal narrow, deeply notched and recurved: siphonal fasciole thick, sloping toward the right, delimited above by the deep fossa. Color yellowish white, with a faint white band connecting the basal crests, a slightly darker band just below and weak brown flecking in the shoulder area of the final whorl. Operculum with latero-basal nucleus and jagged outer edge. Height, 22.5 mm, diameter, 14.0 mm.

Type Locality: Off Gorgona Island, Colombia, 3° 01' 25" N, 78° 10' W, 20 fathoms, R/V *Velero* III station 221-34, 12 February 1934, 4 specimens.

Type Material: Holotype, LACM-AHF 1405, 2 paratypes, LACM-AHF 1406, 1 paratype, USNM.

Referred Material: 21 fully mature lots of this species are represented in the AHF and LACM collections from depths of 10-40 fathoms: 11 stations in the Gulf of California, the northernmost station at Isla Partida (28° 53' N); one station on the outer coast of Baja California at Santa Maria Bay; three stations at Banderas and Tenacatita Bays, Mexico; one station, Costa Rica; two stations, Panama; three stations, Colombia, the southernmost station is the type locality. The species is therefore of fairly broad distribution throughout its range, although it may not be considered abundant, the largest lot represented by but five specimens.

Discussion: *Nassarius shaskyi* is related to *N. corpulentus* (C. B. Adams, 1852), and *N. pagodus* (Reeve, 1844), differing from both in having obsolete spiral sculpture on the final whorl, and in having the rib surface concave rather than rounded between the two crests on the body whorl. In *N. pagodus* the siphonal fasciole projects straight down, while in *N. shaskyi* and *N. corpulentus* it tapers toward the right, following the general outline of the base. The species is named for Dr. Donald R. Shasky of Redlands, California, astute collector and student of Panamic mollusks, who first brought the species to my attention.

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(2) Acknowledgments. — During the course of my work with the Panamic archaeogastropods, I have received assistance through correspondence or during visits to each of the above mentioned institutions, and I am grateful to the people in the molluscan divisions of each for the many courtesies extended. I am especially grateful to Dr. Myra Keen of Stanford University for continued help and encouragement. Photographs of 3 of the minute species were provided by the Museum photography department and those of the *Arene* and *Macrarene* species by Roy Poorman of Pasadena, California.

MALACOLOGICAL REVIEW, P. O. Box 801, *Whitmore Lake, Michigan* 48189, *U. S. A.*

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MALACOLOGISTS INTERESTED IN AFRICA. --- During the last week in November 1969, a meeting was held at the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, which was attended by various people interested in the study of land and freshwater mollusks of Africa, south of the Tropic of Cancer, including Madagascar (Malagasy), the adjacent islands and part of Arabia. This group decided to issue a newsletter once a year, beginning in the spring of 1970, giving names and addresses of researchers interested in this region, as well as lists of their papers and current researches, notes on the location of African type specimens in museums, proposed expeditions to Africa, specialized bibliographies and addresses for inquiries. This newsletter will be called *ACHATINA*. Copies of it will be available at no cost to *bona fide* workers who cooperate in this scheme. The terms of reference will be restricted to taxonomy and zoogeography; medical aspects will be outside the area of interest. A long term project is to compile an annotated bibliography of all the papers dealing with non-marine molluscs of this area.

Those interested should contact Dr. J.-J. VAN MOL, c/o Section des Invertébrés non Insectes, Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

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Malacological Review, 1969, 2: 131-136

PROCEEDINGS OF *THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY** 1969

Communications

1. Organization of the spermatozoon of *Agriolimax reticulatus*, the grey field slug. C. J. BAYNE, *University of Michigan, Ann Arbor, Michigan, U.S.A.* [The full-length paper will be published in *Zeitschrift für Zellforschung und mikroskopische Anatomie*].

2. The reproductive system of *Morula granulata*, with anatomical notes on some other muricid gastropods. S.-K. WU, *University of Michigan, Ann Arbor, Michigan, U.S.A.*

3. Studies on some Neritidae (Neritacea: Archaeogastropoda) of the Coleroon estuary, South India. K. GOVINDAN and R. NATARAJAN, *Centre of Advanced Study in Marine Biology, Marine Biological Station of Annamalai University, Porto Novo, Tamilnadu, India.* [Abstract is given below.]

4. Studies on four species of *Theobaldius* (Cyclophoridae: Mesogastropoda) from South India. R. KASINATHAN and R. NATARAJAN, *Centre of Advanced Study in Marine Biology, Marine Biological Station of Annamalai University, Porto Novo, Tamilnadu, India.* [Abstract is given below.]

5. Some chitons from Taiwan. S.-K. WU, *Institute of Zoology, Academia Sinica, Taipei, Taiwan, Republic of China*, and *University of Michigan, Ann Arbor, Michigan, U.S.A.* [The full-length paper will be published in *Malacological Review*.]

6. The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Prosobranchia: Neogastropoda). W. G. PONDER, *The Australian Museum, Sydney, Australia.* [The full-length paper will be published in *Malacologia*.]

7. The morphology of *Alcithoe arabica* (Prosobranchia: Volutidae). W. F. PONDER, *The Australian Museum, Sydney, Australia.* [The full-length paper will be published in *Malacological Review*.]

8. Some abnormalities in tentacles and eyes of *Pachydrobia pellucida* Bavay, 1885 (Gastropoda: Hydrobiidae). C. T. LO, *Haile Sellassie I University, Addis Ababa, Ethiopia.* [The full-length paper will be published in *Venus, The Japanese Journal of Malacology*.]

9. Morphological and cytological studies of the succineid genus *Quickia* from India. C. M. PATTERSON, *Marine Biological Station, Porto Novo, India* and *University of Michigan, Ann Arbor, Michigan, U.S.A.* [The full-length paper will be published in *Malacological Review*.]

10. Systematic relationships of *Radix hamadai*. J. B. BURCH and T. HABE. *University of Michigan, Ann Arbor, Michigan, U.S.A.* and *National Science Museum, Tokyo, Japan.* [The full-length paper will be published in the *Bulletin of the National Science Museum, Tokyo*.]

11. Cytotaxonomic studies of lymnaeid snails. A. INABA, *Mukaishima Marine Biological Station, Hiroshima University, Onomichi P.O., Hiroshima-ken, Japan.* [The full-length paper to be published in *Malacologia*.]

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*International address: c/o Marine Biological Station, Porto Novo, Tamilnadu, India.

12. Cytological studies of Indian mollusks: A caryotype study of three species of *Paludomus* (Cerithiacea: Mesogastropoda). R. NATARAJAN, *Centre of Advanced Study in Marine Biology, Marine Biological Station of Annamalai University, Porto Novo, Tamilnadu, India.* [Abstract is given below.]

13. Cytological studies of Indian mollusks: chromosomes of some opisthobranchs from Porto Novo, South India. R. NATARAJAN, *Centre of Advanced Study in Marine Biology, Marine Biological Station of Annamalai University, Porto Novo, Tamilnadu, India.* [The full-length paper will be published in *Malacological Review.*]

14. Chromosomes of the snail-borne parasite *Fasciolopsis buski* (Trematoda: Fasciolidae). C. T. LO, *Haile Sellassie I University, Addis Ababa, Ethiopia.* [The full-length paper will be published in the *Bulletin of the Institute of Zoology, Academia Sinica.*]

15. Chromosome numbers and electrophoresis of foot muscle proteins of two species of *Radix* (Basommatophora: Lymnaeidae) from India. J. B. BURCH and G. K. LINDSAY, *Marine Biological Station, Porto Novo, India* and *University of Michigan, Ann Arbor, Michigan, U.S.A.* [Abstract is given below.]

16. The immunological response of South African *Bulinus natalensis* antigens to diploid and polyploid *Bulinus* antisera. J. B. BURCH and G. K. LINDSAY. *Museum and Department of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.*

17. Compatibility and host-parasite relationships between *Bulinus* Müller and an Egyptian strain of *Schistosoma haematobium* (Bilharz). C. T. LO, *Haile Sellassie I University, Addis Ababa, Ethiopia* and *University of Michigan, Ann Arbor, Michigan, U.S.A.* [Abstract is given below; the full-length paper will be published in *Malacologia.*]

18. Infection of diploid *Bulinus* s.s. with *Schistosoma haematobium*. C. T. LO, J. B. BURCH and C. H. J. SCHUTTE, *Haile Sellassie I University, Addis Ababa, Ethiopia; University of Michigan, Ann Arbor, Michigan, U.S.A.;* and *Bilharzia Research Unit, South African Council for Scientific and Industrial Research, Nelspruit, South Africa.* [The full-length paper will be published in *Malacological Review.*]

19. *In vivo* removal of bacteria from the hemolymph of the land snail, *Helix pomatia* (Pulmonata: Stylommatophora). C. J. BAYNE and J. B. KIME, *Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.* and *Department of Zoology, University of Washington, Seattle, Washington, U.S.A.*

Abstracts

3. STUDIES ON SOME NERITIDAE (NERITACEA: ARCHAEOGASTROPODA) OF THE COLEROON ESTUARY, SOUTH INDIA[1]

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Abstract

The intertidal molluscs of the family Neritidae are well known for their great adaptability and are commonly seen in marine, brackish and freshwaters along the east and west coasts of India. The present report, initiated to gain information on the evolutionary adaptation and speciation of these fluviatile snails from marine ancestors, is concerned with the reproductive anatomy and breeding habits of 3 species of Neritidae collected from the upper reaches of the Coleroon estuary (Lat. 11° 25' N; Long. 79° 48' E) in peninsular India.

In all the 3 species, *Dostia crepidularia* Lamarck, *Neritina layardi* Lesson, and *Septaria tessellata* (Lamarck), the sexes are separate and the female is triaulic.[2] A comparison of the female reproductive organs in the 3 species shows that *D. crepidularia* shares some common features with *S. tessellata* on the one hand and with *N. layardi* on the other. But *S. tessellata* and *N. layardi* do not share many similarities. Observations on the breeding habits in the 3 species indicate that both *D. crepidularia* and *S. tessellata* are prolific breeders with high reproductive capacities. *N. layardi* seems to have a smaller reproductive capacity. *S. tessellata* lays for a longer period of time than the other 2 species, and produces larger egg capsules, which contain a greater number of smaller embryos that hatch out sooner.

Dostia crepidularia is an intertidal species that is very adaptable, being found in both brackish and fresh waters. It has a very thick, tessellated shell, suggestive of its marine ancestry. *S. tessellata* is also an intertidal species, and like *D. crepidularia*, it is always found at the water surface, aggregated in groups and attached to stones and other objects covered with algal growth. However, *S. tessellata* is confined to the freshwater zone of the estuary. It seems to be perfectly adapted for the fluviatile habit, possessing a relatively thin tessellated shell with an expanded body whorl and a reduced spire which gives the shell a limpet-like appearance. *Neritina layardi* prefers to live submerged and crawls about singly on submerged stones in thick vegetation. It is found near the bottom in the same areas as *Septaria*. *N. layardi* has an olive-coloured, somewhat thicker shell that is smaller in size and is not tessellated as in the other 2 species. Its septum has a wing-like expansion.

Dostia crepidularia and *Septaria tessellata* appear to be closely related, but *Neritina layardi* seems to be closer to *D. crepidularia* than to *S. tessellata*. It is therefore suggested that *S. tessellata* and *N. layardi* both evolved separately from *D. crepidularia* or a similar ancestor.

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[1] Supported (in part) by a Research grant (SFC-7427) from the Smithsonian Institution, Washington, D. C., U.S.A.

[2] The female is triaulic in that there is a gonopore for egg-laying, a vaginal pore for receiving spermatophores, and a 3rd opening, the *ductus enigmaticus*, of unknown function.

4. STUDIES ON FOUR SPECIES OF *THEOBALDIUS* (CYCLOPHORIDAE: MESOGASTROPODA) FROM SOUTH INDIA[1]

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Abstract

Peninsular India has a very rich land operculate fauna with a record of nearly 200 species and 25 genera (Gude, 1921, *The fauna of British India, including Ceylon and Burma*. Mollusca, III. Land operculates. Taylor & Francis, London. 386 p), many of which are endemic. The systematics of these snails is based almost entirely on shell characters: morphology of their soft parts is mostly

unknown. Additionally, almost nothing is known about other aspects of their biology, including their distribution and ecology. Current knowledge of the anatomy and ecology of the operculate land mollusks from other countries is also scanty (Weber, L., 1924, *Z. Naturwiss.*, 60: 397-438; Tielecke, H., 1940, *Arch. Naturgesc.*, 9(3): 317-371; Morton, J. E., 1952, *Trans. Royal Soc. N. Zealand*, 80(1): 69-79; Berry, A. J., 1964, *Proc. zool. Soc. London*, 142(4): 655-663.). The present study is an attempt to increase our understanding of these interesting mollusks, and is intended to lay the groundwork for further studies on the land operculates of India.

The present investigation is on 4 species of *Theobaldius*, and relates to their distribution, habitats and comparative anatomy. The 4 species have an interesting distribution. *Theobaldius* sp.-1[2] occurs at an altitude of 3,000 ft. and above at Courtallam Hills near the southern tip of the Indian peninsula. In the Alagarkoil Hills near Madurai, *Theobaldius* sp.-2 occurs at 1,200 ft., *T. deplanatus* at 2,500 ft. and *T. shiplayi* at 4,000 ft. and above. These latter 3 species can be collected only during the monsoon period (September-November), and are usually found crawling on or in crevices of wet moss-covered rocks, but they are also under humus and decaying leaves, which they eat. *T. deplanatus* is found very commonly associated with 2 other cyclophorid species, *Pterocyclus bilabiatus* and *Cyclophorus jerdoni*, but the other 3 species occur alone.

A comparison of the 4 species has brought out the following:

1. *Theobaldius* sp.-1[2] (Courtallam Hills) and *T. shiplayi* (Alagarkoil Hills) seem to occur only at higher altitudes and have many morphological similarities and few differences which would demarcate them as distinct species. However, *T.* sp.-1[2] is much smaller.

2. Of the 3 species occurring at different altitudes in the same region (Alagarkoil Hills), *Theobaldius* sp.-2[3] (1,200 ft.) is the smallest and *T. shiplayi* (3,000 ft.) is the largest; *T. deplanatus* (2,500 ft.) is intermediate in size. The differences in size, as well as shell and soft anatomy, indicate that *T.* sp.-2[3] and *T. shiplayi* are distinct species. *T. deplanatus* is most different from the other 3 species, especially in shell morphology, soft anatomy, and spermatophores. It also shows one less foot-muscle protein band by polyacrylamide gel electrophoresis. On the other hand, *T. deplanatus* seems to be quite similar to *Pterocyclus bilabiatus* in shell and soft anatomy, with which it occurs in association.

[1]Supported (in part) by a research grant (SFC-7427) from the Smithsonian Institution, Washington, D. C., U.S.A.

[2]Subsequently identified as *T. shiplayi* by the Zoological Survey of India, Calcutta.

[3]Subsequently identified as *T. ravidus* by the Zoological Survey of India, Calcutta.

12. CYTOLOGICAL STUDIES OF INDIAN MOLLUSKS: A KARYOTYPE STUDY OF THREE SPECIES OF *PALUDOMUS* (CERITHIACEA: MESOGASTROPODA)[1]

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Abstract

Paludomus is a genus of India, Ceylon, Indonesia and the Philippines. Almost nothing is known about the biology of any species of this genus, and even the systematic position of the genus is not clear; - it has been variously placed with the Pleuroceridae and the Thiaridae. Preston (1915, *The fauna of British India, including Ceylon and Burma.* Mollusca. Freshwater Gastropoda and Pelecypoda. Taylor & Francis, London. 244 p) has recorded 8 species of *Paludomus* from peninsular India, of which the anatomy (Seshaiya, 1934, *Rec. Indian Mus.*, 36(2): 185-212) and the chromosomes (Jacob, 1959, *Cytologia*, 24(4): 487-497) of only one species, *P. tanschaurica*, is known. The reported occurrence of sex chromosomes of the XY type in males of this species indicates that chromosome studies may be of value in elucidating systematics within the genus. The present study is a comparison of the male and female karyotypes in 3 species of *Paludomus* collected from South India. The occurrence of XY and XO sex-determining mechanisms were found, as well as other differences, in the karyotypes of the 3 species. In *P. acuta* (XO-type) the chromosome numbers 2n=34+X and n=17+X were observed in the males and 2n=34+XX and n=17+X in the females. In *P. stomatodon* (XY-type) the chromosome numbers 2n=34+X+Y and n=17+X+Y were found in the males and 2n=34+XX and n=17+X in the females. *P. monile* has an XO type of chromosomal sex-determining mechanism, with 2n=34+X and n=17+X in the males. Further studies will be directed toward the origin and evolution of sex-determining mechanisms in this genus.

[1]Supported (in part) by a research grant (SFC-7427) from the Smithsonian Institution, and (in part) by grant GB-5601 from the National Science Foundation, Washington, D. C., U.S.A.

15. CHROMOSOME NUMBERS AND ELECTROPHORESIS OF FOOT MUSCLE PROTEINS OF TWO SPECIES OF *RADIX* (BASOMMATOPHORA: LYMNAEIDAE) FROM INDIA[1]

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and
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Abstract

Two of the most widespread freshwater snails in India are *Radix luteola* (Lamarck) and *R. acuminata* (Lamarck). The former usually has been treated as a distinct species, while the latter recently has been considered a synonym of the race *rufescens* of *Radix auricularia* (Linnaeus). Hubendick (1951, *Kungl. Svenska Vetensk.-akad. Handl.*, ser. 4, 3(1): 1-223) showed that *R. luteola* is peculiarly different from most other lymnaeids (except *Lymnaea stagnalis*) by possessing a multifolded prostate gland, and on the basis of this character Walter (1968, *Amer. malacol. Union ann. Reps.*, 1968, 35: 23-25) stressed an assumed similarity to *Lymnaea stagnalis* in refuting the practicality of generic or subgeneric taxonomy in the Lymnaeidae. For this reason, we were interested in comparing this Indian species (*R. luteola*) to (1) the sympatric *R. acuminata*, (2) the European *Radix auricularia*, and (3) the Holarctic *Lymnaea stagnalis*.

We have confirmed the occurrence of a multifolded prostate gland in *Radix luteola* (although it differs in some rather basic details from that of *L. stagnalis*), and that *R. acuminata* has a unifolded prostate gland, the type known for all other *Radix* and for most other Lymnaeidae.

The electrophoretically separated foot muscle proteins (stained with Buffalo Black NBR [Naphthol Blue Black, Allied Chemical Corp.] on acrylamide gel) were compared in regard to their Rf values, assuming for comparative assessment that those proteins having the same Rf values are identical. The electrophoretic patterns of *Radix luteola* and *R. auricularia* were so similar that those 2 species could not be differentiated by these methods. The patterns for *R. acuminata* were slightly different from those of both *R. luteola* (4 out of 16 bands were different[2]) and *R. auricularia* (3 out of 16 bands were different[2]). All 3 species showed a greater dissimilarity to *Lymnaea stagnalis jugularis* (Say) (5 out of 16 bands were different[2]).

Radix luteola and *R. acuminata* both have 17 pairs of chromosomes, the number characteristic of (and in the Lymnaeidae apparently limited to) the widespread Afro-Eurasian genus *Radix* (including *R. auricularia*). *Lymnaea stagnalis* has 18 pairs of chromosomes like most other lymnaeids (except *Austropeplea*, which has 16 pairs).

We conclude that the multifolded condition of the prostate gland *per se* of *Radix luteola* does not relate this species to *Lymnaea stagnalis*. Further, *R. acuminata* should be studied in greater detail before it is relegated to the synonomy of *R. auricularia*.

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[1]Supported (in part) by a research grant (SFC-7427) from the Smithsonian Institution, and (in part) by grant GB-7569 from the National Science Foundation, Washington, D. C., U.S.A.

[2]Counting bands from Rf 0.130 to Rf 1.000.

17. COMPATIBILITY AND HOST-PARASITE RELATIONSHIP BETWEEN SPECIES OF THE GENUS *BULINUS* (BASOMMATOPHORA: PLANORBIDAE) AND AN EGYPTIAN STRAIN OF *SCHISTOSOMA HAEMATOBIUM* (TREMATODA, DIGENEA)[1]

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Abstract

The ability of various bulinine snails to act as intermediate hosts of an Egyptian strain of the blood fluke *Schistosoma haematobium* was investigated, together with factors affecting snail susceptibility and the effect of the parasite on infected snails.

Twenty-eight laboratory bred populations, representing about a dozen species and subspecies of

Bulinus from various parts of Africa and adjacent regions were exposed to *Schistosoma haematobium* under standardized conditions. Snail size varied from 2-4 mm high; temperature ranged from 24° to 26° C; individual exposure from 10 to 20 miracidia; 2 ml of water were provided per snail. Purchased spring water was routinely applied for all purposes. Cercariae emerged (in the traditional "subgenus"[3] *Bulinus*) from *Bulinus truncatus truncatus*, *B. t. rohlfsi*, *B. truncatus* ssp. (W. Aden), *B. coulboisi*, *B. guernei* (all of the *truncatus* species group, with the haploid chromosome number n=36) and from *Bulinus* sp. (n=72), and, (in the subgenus "*Physopsis*," or *africanus* group) from *B. globosus*. None were obtained from *B. tropicus* and several populations of *Bulinus* sp. belonging to the *tropicus* species group (*Bulinus* s.s. with n=18) and from *B. forskalii* and *B. scalaris* (both subgenus "*Pyrgophysa*"), although in the latter species mother sporocysts grew and persisted for about 2 months without liberating daughter sporocysts. Attention is drawn to the fact that within *Bulinus* s.s. only the polyploids were susceptible, while those with the basic chromosome number of 18 were refractory. Although South African *B. globosus* showed the highest infection rate (76%), *B. guernei* from Gambia (35% infected) was found to be the most suitable host for the maintenance of the parasite as regards ease of breeding, survival, infectivity and cercarial output. The order of suitability for establishing the life cycle among the receptive *Bulinus* s.s. was: good - *B. guernei* (Gambia), *B. truncatus* ssp. (W. Aden) and *B. t. truncatus* (Iran); fair: - *B. t. rohlfsi* (Mauritania), *B. t. truncatus* (Corsica), *B. t. truncatus* (Sudan), *B. t. rohlfsi* (Ghana) and *B. coulboisi* (Tanzania); poor - *B. t. truncatus* (Egypt) and *B.* sp. (n=72, Ethiopia). That our laboratory strain of *B. truncatus* from Egypt (3% infected) was less susceptible than practically any other receptive snail (except for *B. globosus* from Mozambique with 2%) demonstrates that local snail-parasite specificity need not necessarily develop and that snails originating from the same geographical area as the parasites are not always more compatible with them than snails from other areas.

A new species of ameba belonging to the genus *Hartmannella* (C. S. Richards, pers. comm.) was found in some specimens of *Bulinus globosus*; it possibly reduces the schistosome infection in these snails.

To determine the best success of the parasite, several factors affecting the susceptibility of snails were studied in *Bulinus guernei* under a standard set of conditions, varying only the factor under investigation. Generally higher infections were obtained under the following conditions: high alkalinity (optimum results: 49% at pH 9.6); high temperature (67% at 30° C, but less at yet higher temperatures, and negative below 10° C); large miracidial dose (70% at 60+ per snail); in young snails (maximum of 67% in surviving 3-day old snails; however, because of high mortality, snails 1-2 weeks old yielded the maximum of infected specimens); in snails fixed in position (54%), when extended snail body exposes a maximum area, and when anesthetized (81%), presumably because of lesser mucus secretion coupled with extension and immobility.

Infection did not retard growth of snails. Mortality of infected snails over 3 days old, before the onset of cercarial emergence, was not higher than in uninfected snails. No infected snail survived beyond 32 weeks. Infected snails produced from 7 to 100 times (av. 15 times) fewer eggs than uninfected ones and abnormalities were 17 times as frequent. The spawn showed several types of abnormality, singly or in combination, such as lack of eggs in the gelatinous matrix, small size of ovum, lack of embryo, location of embryo outside the egg membrane, polyembryony, presence of cercariae in egg-mass or egg.

Cercarial incubation periods were shorter and more uniform when snails were kept at high temperatures (23 days at 30° C; 35-49 days at 24° C). The peak of cercarial emergence was reached 1-2 weeks after the first shedding and the numbers shed daily fluctuated greatly thereafter, depending on temperature (optimal at 35° C, suppressed at 40° C) and light, as well as on the intensity of infection, health of snail and aquatic conditions. The infection was partially "cured" when infected snails were kept at 35-37° C for a week, as evidenced by decreased cercarial output and increased oviposition. Estimated maximum daily and total shed from a snail was about 2,500 and 20,000 cercariae respectively. Infected snails of a larger size survived longer, laid more eggs and produced more cercariae than smaller snails.

More snails produced male cercariae than they did female cercariae, the female:male ratio being 1:2.6. Only when a snail was heavily exposed to miracidia did bisexual infections appear, at a frequency of 7% (10 miracidia) and 9% (20 miracidia).

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[1] This note summarizes work done for a doctoral dissertation during the years 1966-1968, and shortly to be published in full in MALACOLOGIA. The investigation was supported, in part, by a U.S. Public Health Service Training Grant (5-T1-AI-41) from the National Institute of Allergy and Infectious Diseases, and, in part, by a grant (DA-49-193-MD-2651) from the U.S. Army Medical Research and Development Command.

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[3] The 3 traditional subgenera, though nomenclaturally not strictly correct, and therefore usually replaced by a number of species groups, are nevertheless here indicated for convenience of reference.

Malacological Review, 1969, 1: 137-142

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A malacological journal not included in the "Contents of Malacological Periodicals, 1967" (*Malacol. Rev.*, 1: 137-181) was the *Proceedings of the National Shellfisheries Association* (first published material was for the year 1931).[1] Also, *Lavori della Società Malacologica Italiana*, although not actually a journal but a bound set of collected reprints of the most important malacological works published each year in Italy, was not included in the "Contents. . ." for 1967. Contents of these 2 publications are included here with permission of their editors.

1967 PROCEEDINGS

NATIONAL SHELLFISHERIES ASSOCIATION

Volume 58

OFFICIAL PUBLICATION OF THE NATIONAL SHELLFISHERIES ASSOCIATION; AN ANNUAL JOURNAL DEVOTED TO SHELLFISHERY BIOLOGY

EDITOR

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[1] Although the *Proceedings of the National Shellfisheries Association* also lately includes papers on Crustacea, the majority of its articles and abstracts relate to mollusks.

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The current contents of major malacological periodicals, as shown by their tables of contents, are herewith reproduced as a service to our readers, especially to those who do not have access to larger libraries that subscribe to some or all of these publications. Some malacological publications that are published occasionally rather than periodically, have not been included in this issue, but their contents may be included in future numbers of *MALACOLOGICAL REVIEW*. — J. B. B.

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[1]Country in or from which the journal is published.

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[3]Printed in the U. S. A. and India, but edited internationally and directed to the international community of malacologists.

[4]The first published materials available from the National Shellfisheries Association are for the year 1931, and are printed on "micro cards." The first issue of the *Proceedings* similar to its present form was Vol. 45 for the year 1954, published in 1955. That was the first issue to receive a volume number, a number which was assigned according to the number of years the Association had been in existence. The Association was first organized in 1909 and called the "National Association of Shellfish Commissioners," and the retroactive designation of volume numbers assigns Vol. 1 to that year. Thereby, the *Convention Papers* for the year 1931 are Vol. 23 by retroactive assignment. In 1930 the organization was renamed the "National Shellfisheries Association." No convention was held or annual reports issued in 1945.

According to the current Editors of the *Proceedings of the National Shellfisheries Association*, Arthur S. Merrill and William N. Shaw, the early numbers apparently came out as handouts in the form of *Convention Papers* or *Convention Addresses*. The best of these papers from 1931-1949 were selected and put on micro cards, as also were all annual issues from 1950-1960 (Vol. 51). Complete mimeographed *Convention Papers* were distributed for the years 1950-1953. Beginning with the *Proceedings* for 1954 (Vol. 45), and continuing through 1964 (Vol. 55), the papers were edited and published in offset from typewritten copy. In 1965 (Vol. 56) the format was changed to its present form. Some back issues of the *Proceedings* are available for purchase from the Custodian, National Shellfisheries Association, c/o Biological Laboratory, Bureau of Commercial Fisheries, Oxford, Maryland, 21654, U. S. A.

[5]Each volume of the *Lavori della Società Malacologica Italiana* is a bound set of collected separates or reprints of the most important works on malacology published in Italy during the previous year.

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for 1968

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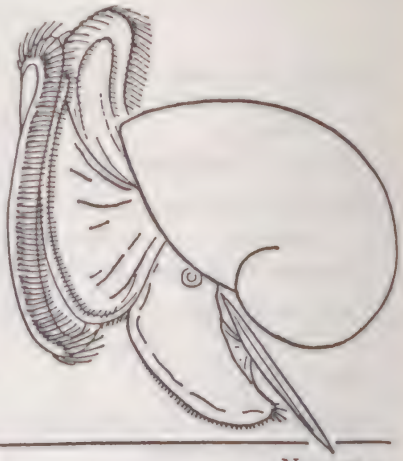

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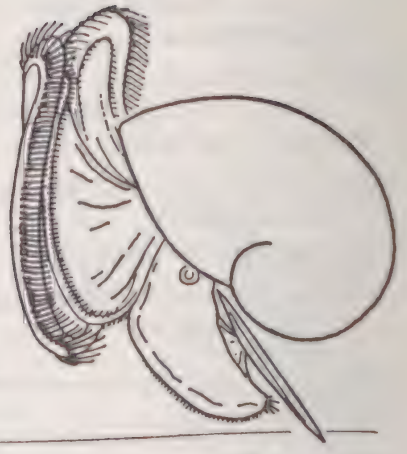

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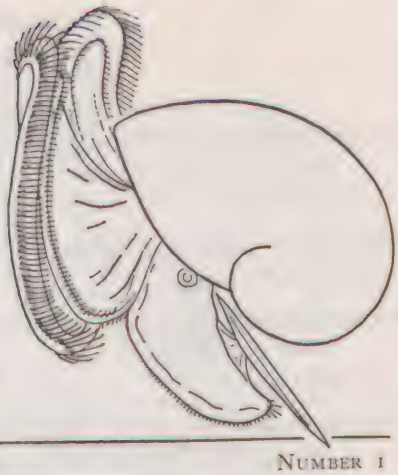

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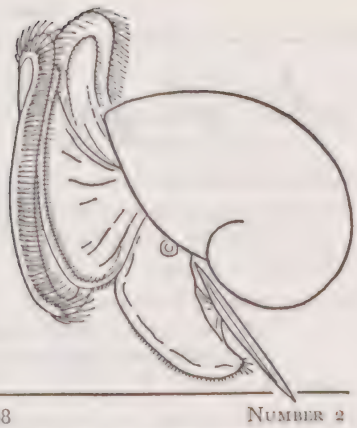

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p 6, Fig. 9 a, b, c: "tentacle retractor" should read "tentacle assembly", which includes the tentacle retractor muscle, tentacle nerve and optic nerve.

p 16, Fig. 1: the 5 shells from left to right are a, b, c, d and e respectively.

p 16, Fig. 2: the 2 shells from left to right are a and b respectively.

p 16, Fig. 3: the 2 shells from left to right are a [*Austropeplea*] and b [*Radix*] respectively.

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